THE ECOLOGY OF *GALAXIAS VULGARIS* (PISCES : SALMONIFORMES : GALAXIIDAE) IN THE RIVER GLENTUI, CANTERBURY, NEW ZEALAND.

A thesis presented for the degree of Doctor of Philosophy in Zoology at the University of Canterbury, Christchurch, New Zealand.

by

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1973

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Chapter I

INTRODUCTION

The family Galaxiidae is considered to belong to the order Salmoniformes (Greenwood et al, 1965) and together with the families Aplochitonidae and Retropinnidae forms the suborder Galaxiodei. The family Salangidae was considered by Greenwood et al (loc. cit.) to belong to the Galaxioidei, though Weitzman (1967) and McDowall (1969b) have since indicated that it should be a group distinct from the other three families. The Galaxioidei form a compact southern temperate radiation related to and comparable with the northern temperate diadromous salmoniforms. The family Galaxiidae is widespread, with species occurring in Australia, New Zealand, South America and South Africa and also on many islands near these land masses (Stokell, 1953; Darlington, 1957; McDowall, 1970).

The taxonomy of the Galaxiidae has been the subject of much confusion. However, the work of Stokell (1938, 1945, 1949, 1959) and McDowall (1967, 1969b, 1970, 1972) has greatly clarified the systematics of the New Zealand fauna. Thirteen species are now recognized in New Zealand (McDowall, 1970, 1972) and are divided into two genera, namely Galaxias with ten species and Neochanna with three species. Apart from Galaxias maculatus, which forms the basis of a commercial and sport fishery (see Hopkins and McDowall, 1970), little attention has been given to the ecology of galaxiids. Most freshwater fish studies in New Zealand have been concerned with the ecology of the introduced salmonids, particularly Salmo trutta, Salmo gairdneri and Oncorhynchus tshawytscha (see, for example, Phillipps, 1924; Philips, 1929; Parrot, 1932; Percival, 1932; Hobbs, 1937, 1940, 1948, 1953; Allen, 1951; Percival and Burnet, 1963; Lane, 1964; Burnet, 1968, 1969a, b; Hopkins, 1970; Hardy, 1972) which form the basis of a thriving sport fishery (Watkinson and Smith, 1972). As pointed out by McDowall (1968b), a number of galaxiids, particularly G. divergens, G. vulgaris, G. paucispondylus, G. fasciatus and

G. argenteus, do not seem to be compatible with the introduced salmonids and appear to be adversely affected by their presence, although the interactive mechanisms are not understood. To understand the interrelations between the native and introduced fish faunas, it is first necessary to have an understanding of the ecology of the native fish. This study was undertaken in order to provide such an understanding of one of the species considered by McDowall (1968b) to be incompatible with the introduced Salmonids, viz. Galaxias vulgaris.

Galaxias vulgaris is restricted to the South Island of New Zealand and is found in most of the major river basins to the east of the Southern Alps and also in the Upper Buller River System on the west of the Alps. It is not usually found in streams entering lakes (Stokell, 1949; McDowall, 1970). It was first described by Stokell (1949) who also (Stokell, 1959) described Galaxias anomalus which has since been synonymized with G. vulgaris by McDowall (1970). It is a rather variable species, the variability being caused by its wide range and the fact that it is confined to freshwater and is therefore unable to disperse from one river system to another by marine routes. Gene flow is therefore restricted to population exchanges by means of stream capture and perhaps by unusual flood conditions, when waters of two or more river systems are temporarily confluent (McDowall, 1970).

Galaxias vulgaris is found in the fast or broken water of rivers and streams, where it occurs beneath and between boulders. Benzie (1961 unpublished, 1968d) compared the life histories of G. vulgaris and G. maculatus, with special emphasis on embryology, growth rates and breeding cycles.

The aims of the present study were:

1. To establish the basic population parameters of G. vulgaris in one locality.
2. To examine the stability and range of movement of the population.
3. To investigate the interrelations of G. vulgaris and

cohabiting fish species, with a view to understanding the relationships between the native fish, particularly the Galaxiidae, and the introduced Salmonids, particularly S. trutta.

The first part of this thesis is concerned with the age, growth and condition of G. vulgaris. Subsequent sections, in order, deal with breeding biology, home range and movement, food habits, feeding mechanisms, the relationship between dorsal brain pattern and ecology, and interspecific relationships.

Chapter II

THE STUDY AREA AND GENERAL METHODS OF STUDY

1. Study Area

This investigation into the ecology of Galaxias vulgaris was carried out in the River Glentui, Canterbury, New Zealand. The River Glentui arises at an altitude of approximately 840 m and flows into the River Ashley at a point (latitude 43°14'S, longitude 172°18'E) 180 m above sea level. It originates in a forest of mountain beech, Nothofagus solandri, and in its lower reaches flows through cultivated farm land. Its largest tributary is the Bald Hills Stream which enters the River at an altitude of 300 m. A number of smaller tributaries enter the River carrying run-off from the surrounding hills. (See Figs. 1 and 2).

(1) Local climate

The prevailing winds are from the north-west and are relatively warm. Air temperatures in 1970 ranged from a summer maximum of 34.4°C to a winter minimum of -3.9°C, and similarly in 1971 the range was between 33.5°C and -4°C (N.Z. Meteorological Service, pers. comm.). Mean, maximum and minimum air temperatures from June 1970 to May 1971 are presented in Fig. 3a.

Mean annual rainfall (1947-70) for the area is 108 cm and the period of maximum rainfall is typically in spring and early summer from October to January (N.Z. Meteorological Service, pers. comm.). Rainfall from June 1970 to May 1971 totalled 88 cm and was heaviest in spring and early summer (Fig. 3c). Rainfall from June 1971 to May 1972 totalled 98.5 cm and followed the typical pattern except that there was an abnormally high rainfall of 21.9 cm in May 1972.

(2) River Glentui

The distance between the origin of the River Glentui and its point of entry into the River Ashley is approximately 9.5 km. Near its origin there is a series of waterfalls ranging in height from

FIGURE 1. An aeriel view of the study area (Crown copyright).

Key to letters:

a – g River Glentui.

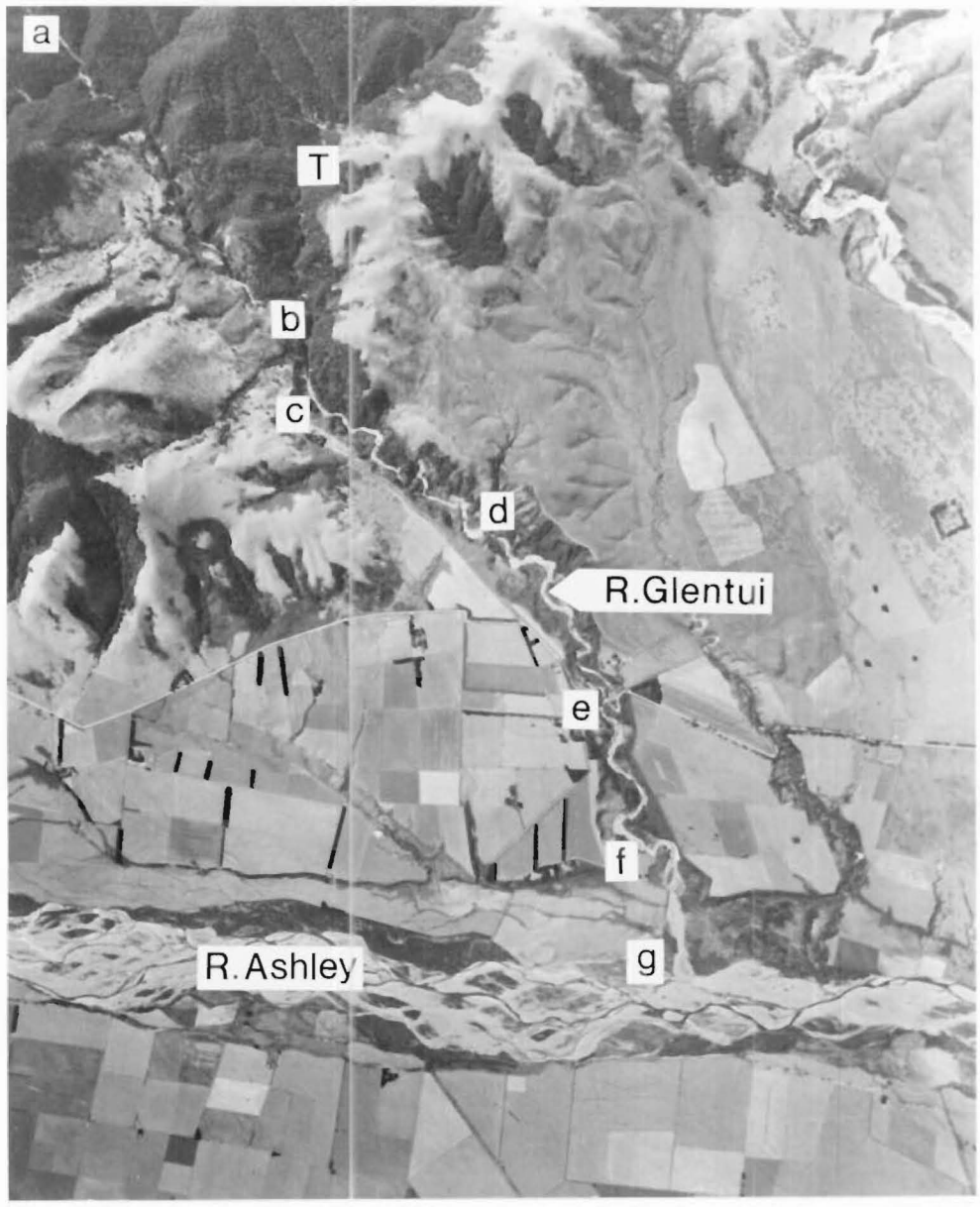
b Position of the most downstream waterfall (height = 2.5 m).

c – d Section of River from which samples were taken for the elucidation of population parameters and food habits.

e – f Section approximately 490 m long in which the home range investigation was carried out, (e marks the upstream end of section U5; f marks the downstream end of D8 – see section 1. of Chapter V for explanation).

d – e and f – g Sections from where fish used in laboratory experiments were obtained.

T Bald Hills Stream – the main tributary of the River Glentui.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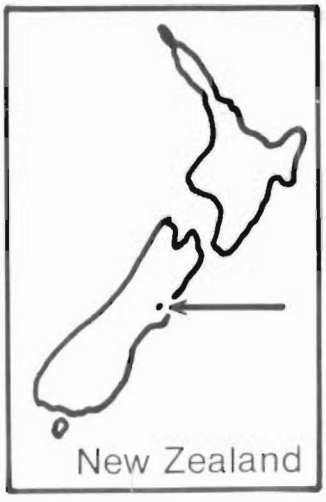

New Zealand

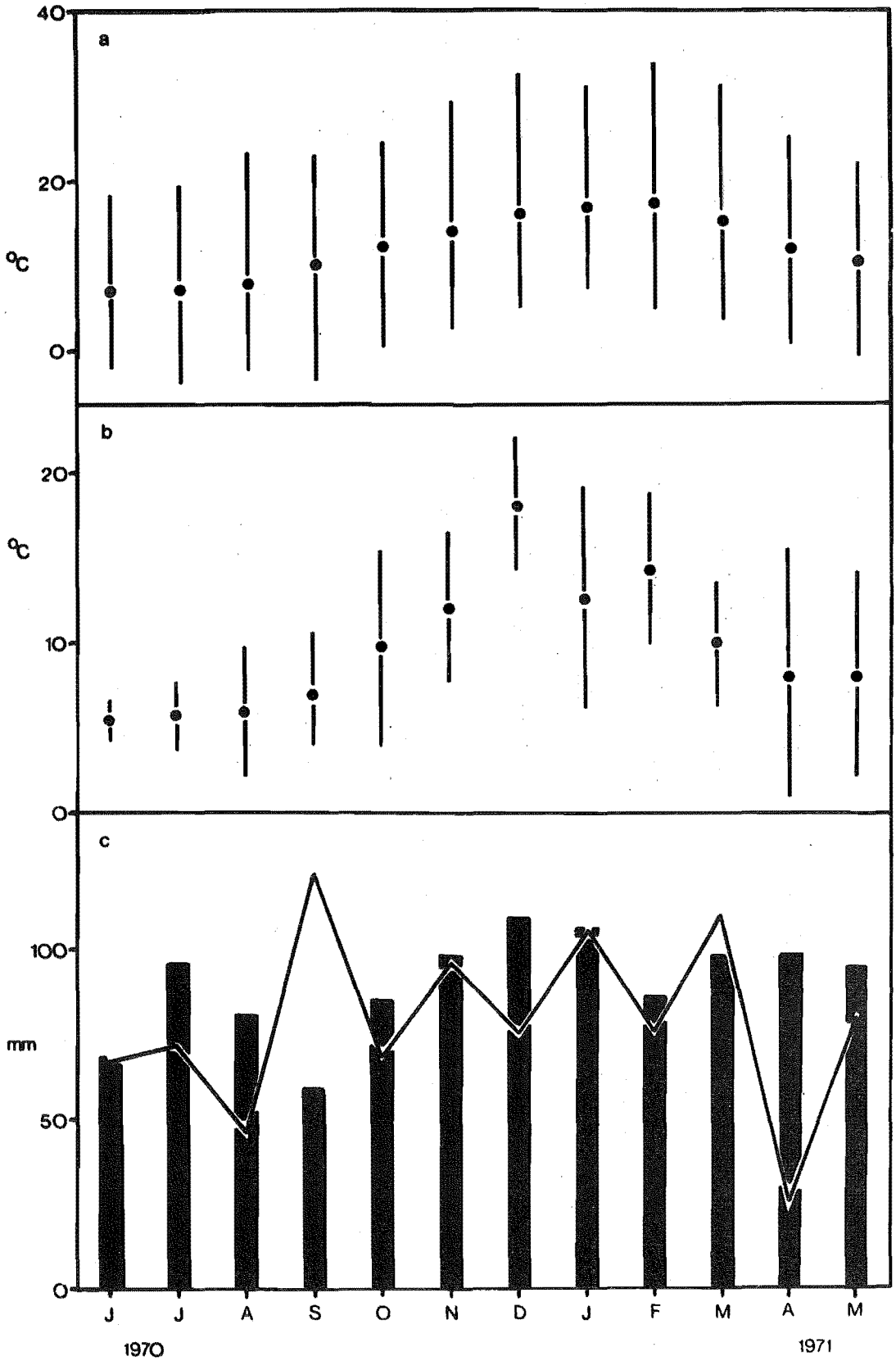
FIGURE 2. A section of the River Glentui (near position c in Fig. 1). (Photograph – R. M. Ogilvie).

FIGURE 3. Temperatures and rainfall recorded in the study area from June 1970 to May 1971.

a. Mean monthly air temperatures.

b. Mean monthly water temperatures. In both a and b the temperature range is indicated by vertical bars.

c. Monthly rainfall (graph) and mean monthly rainfall from 1946 to 1970 (histogram).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2.5 m to 24 m. Regular sampling was confined to a 4.8 km stretch of the River below the waterfalls. This sampling area consisted mainly of riffles interspersed with quiet stretches (see Fig. 1.). During the course of the study, water depth varied markedly, from 2-3 cm in riffle areas to 70 cm in pools formed behind obstacles such as fallen trees. The width of the River varied from 1 m in the narrowest channels to 9 m in the more open stretches. However, there was great variation in both depth and width. The above figures are approximations based on measurements taken throughout the sampling period; more detailed figures for these characteristics in specified parts of the River are given in Chapter V.

The geological deposits over which the River flows are of two main types. Above an altitude of 305 m they are strongly indurated and consist mostly of graded-bedded greywacke and argillite. Below 305 m the deposits consist mainly of glacial outwash gravels (Gregg, 1964).

The river bed is composed of fine gravel in the quiet stretches with large boulders, up to 70 cm in diameter, occurring in the riffle areas. Fine mud is present but is restricted to the quiet backwaters and deep pools. During the investigation water velocity varied from 0 m/sec at the bottom of the deep pools to a mean value of 0.4 m/sec in the riffle areas. Surface water was present in the main channel of the River throughout the investigation, although in the autumn of 1971 surface water was absent from a number of other local rivers, including parts of the River Ashley (North Canterbury Acclimatization Society, Annual Report for 1971). Although the Glentui is more stable than many other similar rivers in Canterbury, severe floods after heavy rainfall often cause the water velocity in the narrowest riffles to exceed 3 m/sec. Such flooding precludes the establishment of macrophytes in the main channel and has a marked effect on the character of the river bed. Apart from isolated stands of Myriophyllum in the quieter backwaters, the only plant cover in the River is that provided by fallen trees and other debris of terrestrial origin carried down by floods.

During the study the pH of water in the middle of the regular sampling area varied from 6.8 to 7.3. The water was relatively soft, alkalinity ranging from 0.838 to 1.24 mg HCO_3^-/l. Conductivity at 25°C varied from 128 to 150 μmhos/cm (Stout, pers. comm.), a moderate value for the Canterbury region. Stout (pers. comm.) found low values from 38 to 55 μmhos in Ribbonwood Stream flowing into Lake Grasmere (altitude 600 m). On the other hand, Winterbourn, Alderton and Hunter (1971) reported conductivities exceeding 400 μmhos in the more polluted parts of the lower Waimakariri River system.

Water temperatures were taken with a maximum-minimum thermometer at monthly intervals from June 1970 to May 1971 and at irregular intervals from June 1971 to April 1972. All readings were made in the middle of the same riffle area after the thermometer had been in position on the river bed for 24 hours. Fig. 3b shows the mean, maximum and minimum water temperatures recorded from June 1970 to May 1971. Ice was present on standing water at the sides of the River for short periods in the winters of both 1970 and 1971, but did not occur in the main channel.

(3) Biological characteristics

Diatoms, of which Gomphonema was the most abundant (Flint, pers. comm.), were present on most of the boulders on the river bed. As mentioned in the previous section, Myriophyllum was the only macrophyte found in the River.

The invertebrate fauna of the River was dominated by insects in various phases of their life cycles. These included Archichauliodes diversus (Neuroptera); species of Stenoperla, Aucklandobius, Zelandoperla (Plecoptera); species of Nesameletus, Deleatidium, Zephlebia, Oniscigaster, Ameletopsis and Coloburiscus humeralis (Ephemeroptera); Hydropsyche colonica, Hydrobiosis, Helicopsyche, Pycnocentrodes, Pycnocentria, Hudsonema, Beraeoptera, Triplectides, Oxyethira and Olinga (Trichoptera); species of Helodidae and Elmidae (Coleoptera); the dipterans Austrosimulium multicorne and Austrosimulium ungulatum (Simuliidae), species of Orthocladiinae,

Tanytarsini, Anatopynia and Maoridiamesa harrisi (Chironomidae) and species of Dixidae, Tabanidae and Tipulidae; species of Anisops and Microvelia (Hemiptera).

Other invertebrates were the gastropod Potamopyrgus antipodarum and Gordius pachydermus (Nematomorpha). No crustaceans were found in the sampling area. Terrestrial arthropods and lumbricids together with plant debris were frequently found in the drift.

Apart from G. vulgaris, other fish species found in the sampling area were the upland bully, Philypnodon breviceps; the long-finned eel, Anguilla dieffenbachii; the short-finned eel, Anguilla australis and the brown trout, Salmo trutta. All of the fish species except S. trutta are native to New Zealand.

Black shags, Phalacrocorax carbo, were occasionally seen near the River. These birds are known to take galaxiids, eleotrids, salmonids and anguillids in New Zealand inland waters (Falla and Stokell, 1945; Dickinson, 1951; Boud and Eldon, 1960; Duncan, 1968), but they were not considered to be important predators of fish in the River Glentui.

2. General Methods

(1) Sampling Programme

Data on growth in length and weight, age, gonad weight, maturity, fecundity, feeding habits and home range were obtained for G. vulgaris sampled in the River Glentui from June 1970 to April 1972.

Regular samples of G. vulgaris were taken from a 1.5 km stretch of the River every 28 days from June 1970 to May 1971. All fish in these samples were measured to provide monthly information on growth in length. A stratified subsample of at least two fish of each sex in each 5 mm length-class was then taken and preserved in 10% formalin, the remainder being returned to the River. The subsampled fish were later weighed and aged; their gonads were removed, weighed and their condition noted; fat deposits were estimated and stomach contents removed for analysis. Table 1 shows the number of fish in each sample used in the above studies; it includes only those fish caught in normal adult habitat (see Chapter V) and does not include young-of-the-year fish less than 30 mm long. All fish in the July and August 1970 samples

were removed from the River for fecundity estimates and determination of the age composition of spawning fish. All young-of-the-year fish in sample 11 (April 1971) were removed for maturity studies.

TABLE 1. Regular samples of G. vulgaris used to provide data on population parameters and food habits.

Regular sample number	1970	No. of fish in sample	Regular sample number	1971	No. of fish in sample
1	June, 27-28	89	8	Jan., 16-17	146
2	July, 25-26	139	9	Feb., 6-7	128
3	Aug., 22	55	10	Mar., 6-7	176
4	Sept., 19-20	100	11	Apr., 3-4	262
5*	Oct., 17	24	12	May, 1-2	180
6	Nov., 14-15	171	13	May, 29-30	163
7	Dec., 12-13	175			

* Unfavourable fishing conditions after heavy rainfall.

During the sampling periods of February and May 1971, collections were made of the other fish species inhabiting the River. A further sample of all fish species in the River was taken in November 1971. These fish were immediately anaesthetized and preserved in 10% formalin for subsequent analysis of their stomach contents.

In addition to the above regular collections a number of other samples were taken during and after the breeding season (from July to January) in 1970-71 and 1971-72. From these samples information was obtained on reproductive biology and the ecology of recently-hatched fish, 1,366 of which were preserved in 10% formalin for growth and food studies.

Collections of fish for laboratory experiments were made throughout the study period.

All of the above-mentioned collections were made outside that

part of the River used for the investigation of home range and movement of G. vulgaris. Information on this aspect of the study was derived mainly from samples taken from a 487 m stretch of the River from March 1971 to April 1972.

Figure 1 shows the River Glentui and those sections of it sampled during the present study.

Only general methods are considered in this section. More detailed methods concerning particular aspects of the study are given in each chapter.

(2) Electric fishing

Most samples were obtained using portable electric fishing equipment. Power was supplied by a Honda E300 generator via a 12 volt battery. Positive pulses were passed to the water through an electrode held by the operator. An earth return system consisting mainly of a long, flexible, metal cord completed the circuit. The current loading could be altered to four settings with maxima of 0.22, 0.4 and 0.5 amps and a setting which could not be overloaded. The output was a positive square wave pulse at about 100 c.p.s. with peak voltages of 300, 150, 100 or 50 volts as required. A second pulse with an 80% on duty cycle at about 3 c.p.s. was imposed on this (Woods, 1967 unpublished).

The use of electric fishing equipment, briefly reviewed by Hynes (1970a), is one of the least selective of fishing methods (Harrison, 1955; Boccardy and Cooper, 1963; Libosvarsky and Lelek, 1965; Lagler, 1968; Johnson, Rinne and Minckley, 1970). However, Schuck (1945), Holton (1953), Saunders and Smith (1954) and Woods (1964) have shown that there is usually some bias towards the larger length classes. The equipment was most effective in the River Glentui where the water was generally shallow and of moderate conductivity, and the substrate of gravel and boulders was of high resistance. Its effectiveness decreased in the deeper pools. The radius of the effective field with the positive electrode at its centre was about 30 cm for fish of 100 mm. Thus, since fish were stunned over quite a small area of the river bed, it was possible to make observations on microhabitat preferences. Under these

conditions all length classes of fish were sampled adequately except recently-hatched G. vulgaris less than 30 mm long which inhabited the still, deep parts of the River. However, these fish were taken easily with dip nets. Only those fish longer than 150 mm, usually S. trutta and Anguilla spp., were "attracted" by forced swimming towards the electrode. Smaller fish were stunned and floated, ventral-side-up, to the surface.

When taking samples, the stretch to be fished was divided into a series of sections each about 10 m in length. Each section was then arbitrarily divided into a number of units each about 1.5 m wide. Each unit was fished by starting at its downstream end and working upstream. When one unit was completed the operator returned downstream and began fishing again at the downstream end of the adjacent unit. This was continued until the width of the River in each section had been fished. Normally each section was fished only once, but in the samples taken for the investigation of home range and movements each section was fished twice, the second fishing following immediately after the completion of the first. A long-handled dip net was held behind the electrode when fishing so that any fish not seen by the operator would be carried into the net by the water current. All stunned fish were removed by dipnet and placed in large plastic containers where they soon recovered from the effects of the shock.

Mortality caused by electric fishing was negligible. That which did occur was because of over-exposure to the electric field as in fish caught between boulders and not immediately seen by the operator. In the home range investigation a few G. vulgaris showed reddening of the caudal peduncle after repeated electric fishings over a period of 12 months. This condition was caused by the rupture of blood vessels in the tail region and is related to the type of pulse produced by the electric fishing equipment (Burnet, pers. comm.). Hauck (1949) reported a similar condition in rainbow trout (Salmo gairdneri) that were shocked with 110 volts alternating current. Spencer (1967), working with bluegill (Lepomis macrochirus), channel catfish (Ictalurus punctatus) and largemouth bass (Micropterus salmoides) exposed to 230 volts A.C. showed that fractures

and dislocations of the vertebral column occurred in the caudal region. Large fish are more susceptible to this type of damage than fish of the size of G. vulgaris used in the present study, the largest of which was 125 mm in length. Fish with ruptured blood vessels in the caudal peduncle did not appear to be at any disadvantage compared with normal fish and in the present study the few affected fish (less than 20 individuals) were treated as normal.

(3) Anaesthetic

After capture and before further handling, all fish were anaesthetized with benzocaine, some properties of which are described by McErlean and Kennedy (1968). A saturated solution of benzocaine in absolute alcohol was added to a shallow tray of water containing the fish. Dosage depended on temperature and was adjusted so that anaesthesia was complete in three minutes. Complete anaesthesia was indicated by total loss of motor coordination and equilibrium.

Regurgitation of stomach contents by fish when placed in formalin was prevented by prior anaesthesia.

(4) Measurement of length and weight

Total length of fish was measured in two ways depending on the shape of the tail. Fish with a rounded tail, with the median rays longest, e.g. Anguilla spp. and P. breviceps, were measured from the tip of the snout to the end of such rays. Fish with an emarginate or forked tail, e.g. G. vulgaris and S. trutta, were measured from the tip of the snout to the centre of the fork of the caudal fin. This latter total length measurement has been variously called the median length, mid-caudal length or fork length (Carlander and Smith, 1945; Ricker and Merriman, 1945).

Measurement of the total length of most fish was made to the nearest 0.1 mm using a measuring board fitted with a vernier scale designed by Woods (1968). Large eels were measured against a tape measure to the nearest 5 mm. Throughout this work, length refers to total length (TL) unless otherwise indicated.

Wet weight of both fresh and formalin-preserved fish was measured to the nearest 1 mg. Fish were weighed whole; gonads were then removed and weighed to the nearest 0.1 mg.

The effect of formalin on the length and weight of G. vulgaris was determined from a sample of 20 fish held in 10% formalin for 245 days (Table 2).

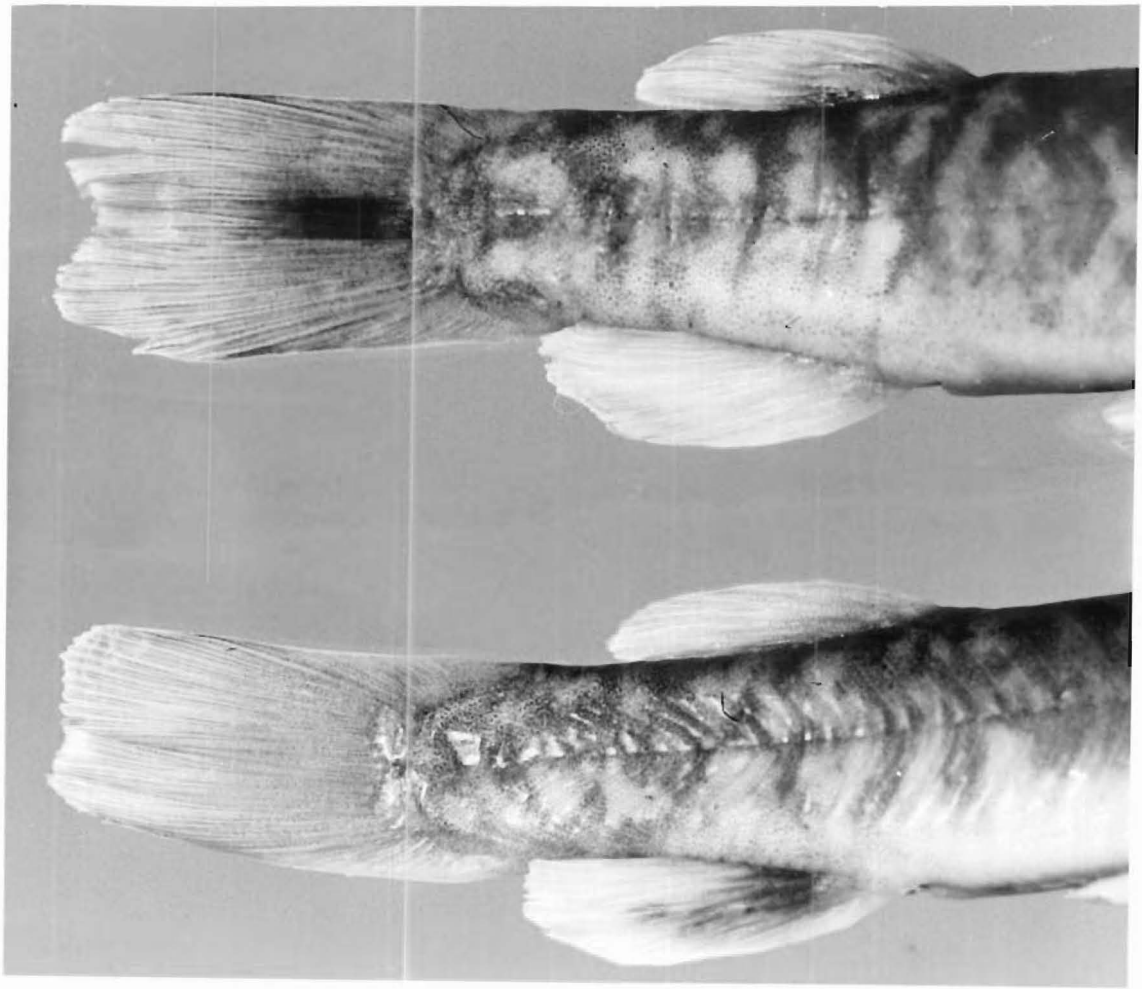
TABLE 2. The effect of 10% formalin on length and weight of G. vulgaris. Sample size = 20. (CL = confidence limits)

Days in formalin	Mean percent of fresh length	95% CL of mean	Mean percent of fresh weight	95% CL of mean
0	100		100	
0.5	95.61	0.662	105.05	1.044
1	95.15	0.691	106.98	0.860
2	94.98	0.674	106.81	1.103
4	94.89	0.698	106.14	0.829
6	94.82	0.728	105.68	0.870
8	94.82	0.728	105.73	0.957
12	94.79	0.765	105.42	1.139
20	94.68	0.686	105.06	0.986
30	94.42	0.674	104.50	1.069
60	94.23	0.641	103.80	1.052
90	94.31	0.737	103.82	0.998
120	94.28	0.808	103.13	1.096
245	94.08	0.742	102.78	0.980

The greatest changes occurred in the first 24 hours, length decreasing and weight increasing. The trend continued for length at a slower rate throughout the experiment. However, after an initial sharp increase, weight decreased towards the initial fresh value. This probably reflects chemical changes brought about by the formalin, which affect the osmotic strengths of fluids within the body and within the cells (Parker, 1963). Since most measurements of preserved G. vulgaris were taken approximately one week after preservation the most commonly used correction factors were: fresh weight = 0.948 x preserved weight

fresh length = 1.055 x preserved length

FIGURE 4. Marked G. vulgaris recaptured after 11 months in the River Glentui, showing caudal (upper fish) and anal (lower fish) Alcian Blue marks. (Photograph - E. J. Buckley)



(5) Sex determination

From May to November, during the ripening, spawning and post-spawning stages of the reproductive cycle, adult G. vulgaris were sexed externally using a dissecting microscope at low magnification (X6.3). During this period the anatomy of the genital region differs between males and females. Males possess a papilla at the tip of which is the genital opening. Females lack a papilla and the genital region is much more bulbous than in males. The male papilla can be made to protrude by flexing the body. This method of sex determination was unreliable during the resting and early-ripening stages of the reproductive cycle, from December to April. At this time the female genital region is less bulbous and the male papilla is less distended and cannot always be made to protrude. Sex determination of young-of-the-year fish by this method was unreliable because, although mature males were easily identified, immature males could not be distinguished from females. Microscopic examination of gonads was used to sex all fish which could not be sex externally.

(6) Marking

Fish used in laboratory experiments and in the home range investigation in the River Glentui were marked with Alcian Blue dye at a concentration of 65 mg/ml (as recommended by Kelly, 1967), using a jet inoculator, as described by Hart and Pitcher (1969). Pontamine Fast Pink was also tried in laboratory situations, but marks produced by this dye faded after three weeks. Alcian Blue marks were long-lasting and were distinguished readily after 11 months in both laboratory and field conditions (see Fig. 4). The fins, both paired and median, proved to be the best marking sites. When marking, fish were anaesthetized and laid flat on a wet cloth; the dye was administered with the nozzle of the inoculator 2-3 mm from the marking site. After marking, excess dye was removed by dipping the fish into water. Any unsatisfactory marks were recognized at this stage and, if necessary, fish were marked again. The total lengths of G. vulgaris marked successfully by this method ranged from 50 to 125 mm. Over this range no mortalities were caused by the marking procedure outlined above. Marking was confined to the fins, because marks administered to other parts of the body often proved

fatal. Fish smaller than 50 mm were difficult to mark using the inoculator and often were killed by administration of the dye.

Thus, for fish larger than 50 mm, inoculated Alcian Blue marks proved satisfactory. The marking process was quick and simple, and produced clear, long-lasting marks. Since G. vulgaris is generally nocturnal (see Chapter VI) and spends the daylight hours under and between boulders, the possession of a bright blue mark was considered to be no disadvantage as far as predators were concerned. There was no immediate post-marking mortality and there appeared to be no long-term mortality associated with marking under field conditions (see Chapter V). Growth did not appear to be affected and, from laboratory observations, there appeared to be no effect on locomotion or on behaviour in general.

Chapter III

AGE AND GROWTH

1. Methods of Age Determination

A method of determining the age of individual G. vulgaris was fundamental to an understanding of the life history of the species. Methods for the determination of age in fish are numerous and the extensive literature has been reviewed by Chugunova (1963) and Tesch (1968). Benzie (1961, unpublished) described the otoliths of Galaxias maculatus. Burnet (1965) was able to age G. maculatus by means of controlled growth experiments, but McDowall (1968a) found that otoliths and length frequency analysis could not be used to age G. maculatus because of its extensive breeding season from September until June. Pollard (1971), working with a landlocked population of G. maculatus, used length frequency analysis with some success but found otoliths to be of little use an an aid to ageing the fish. Hopkins (1971a) used both length frequency analysis and otoliths to age Galaxias divergens but did not validate the use of otoliths for this species. In the present study sagittal otoliths and length frequency analysis were used in combination to age G. vulgaris.

(1) Otoliths

The use of otoliths to age fish depends on changes in the rate of growth or metabolism which are reflected in the otoliths as alternating bands of visibly different material. The sagittal otoliths of G. vulgaris are plano-convex and basically discoidal with a forward projection at the antero-ventral corner. This projection is not well developed in small otoliths but becomes more prominent when the otoliths increase in size.

Both sagittal otoliths were removed from fish subsampled from regular monthly catches in the River Glentui between June 1970 and May 1971, and from recently-hatched fish sampled after the breeding season from September 1970 to January 1971. They were then stored dry in tube vials, together with details of the total length and sex of the fish from which they had been taken.

FIGURE 5. Otoliths of G. vulgaris.

Key to letters:

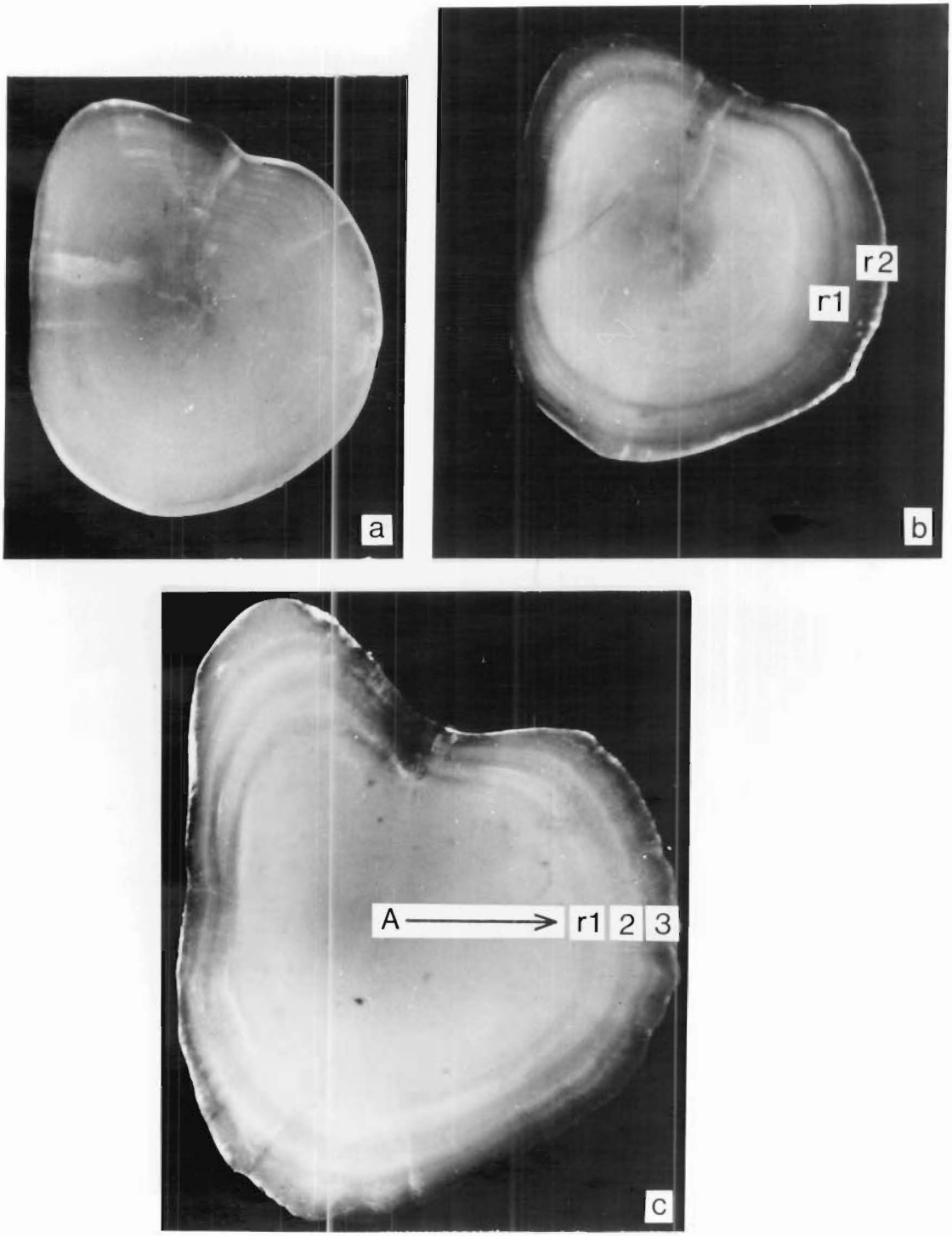
a. From male of TL 56 mm sampled in May 1971. Radius = 0.34 mm.

b. From male of TL 64 mm sampled in November 1970. Radius = 0.43 mm.

c. From female of TL 93 mm sampled in November 1970. Radius = 0.59 mm. The arrow from A indicates the axis along which measurements were made.

Numbers indicate the positions of annuli. See text of section 1. for further explanation.

(Photographs - F. McGregor)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r2
r1
b
A
r1
2
3
c

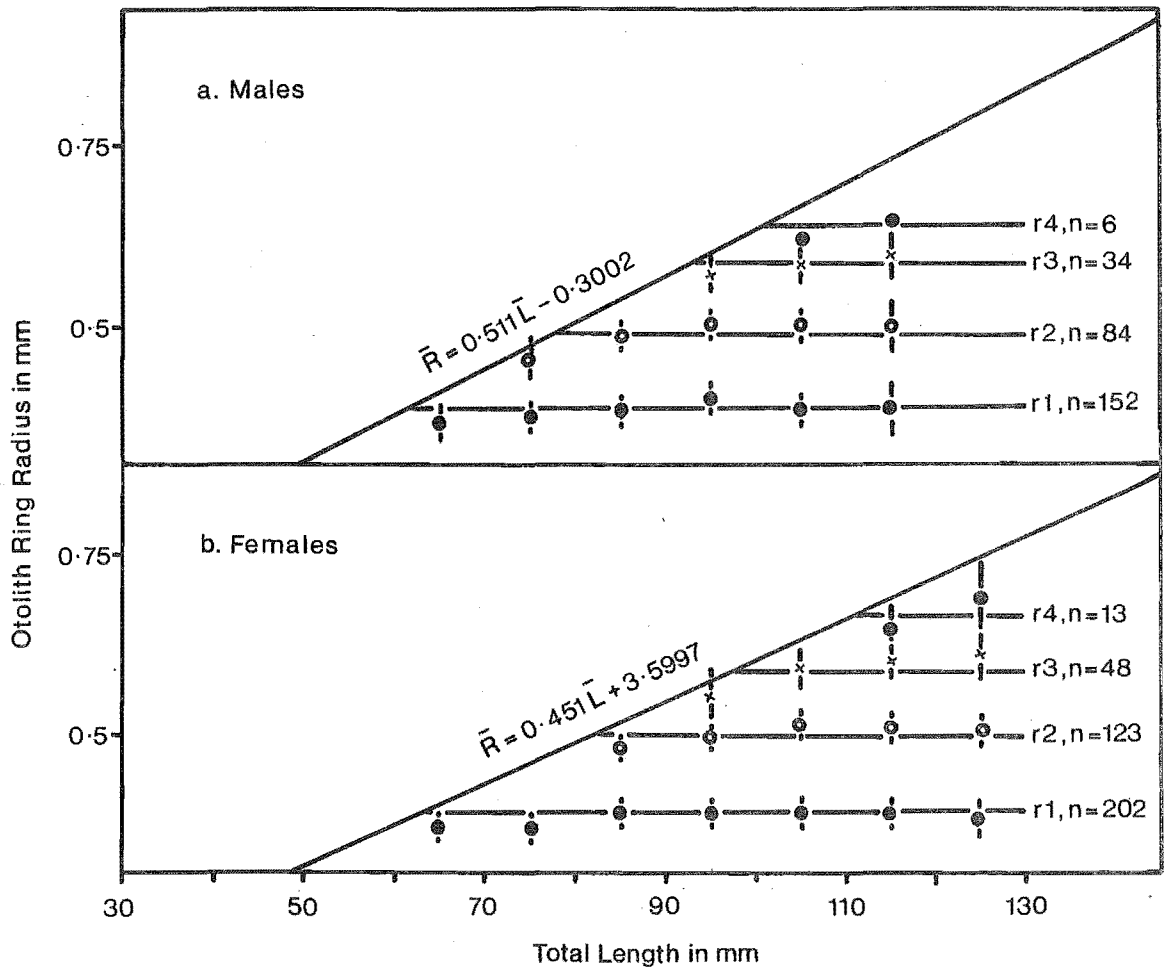
(a) Interpretation of otoliths

Reading of otoliths was carried out under a microscope at X80 magnification; they were immersed in xylol and viewed against a black background using reflected light. With this method a number of opaque (light) and translucent (dark) zones were visible in the otoliths. It can be seen in Fig. 5 that the outer border of each translucent zone forms a distinct ring where it abuts the next outer opaque zone. Since the edges of the otolith are thinner than the central nucleus they often appear translucent and this must be borne in mind when interpreting otoliths.

It is important to distinguish between rings laid down on a regular temporal basis, i.e. primary rings or annuli (see Jensen, 1965), and those which result from non-periodic variation in growth, i.e. secondary rings. Rings were considered to be annuli on the criteria that they were more distinct, were uniformly spaced and extended right around the otolith (Staples, 1971). The consistency of recognition of annuli was tested using the July 1970 sample of 139 fish. In this sample, the number of annuli in each otolith was counted twice, the second reading being six months after the first. Out of 139 otoliths, all but three were read the same on both occasions - a consistency of 97.8%. The criteria for distinguishing annuli were considered therefore to be adequate. Only annuli were used to determine age and the number in each otolith was counted.

In some otoliths two translucent zones occurred close together. On the criterion of spacing they were considered as representing one annulus. Secondary rings were more readily seen in the thin otoliths of young fish. Typically, there were two of these narrow translucent rings. One, surrounding the central nucleus, was formed at total lengths ranging from 12 to 17 mm and coincided with the end of larval life. The other ring formed at total lengths from 30 to 50 mm and coincided with the transition from juvenile to the adult way of life. These rings were considered not to be annuli on the first criterion mentioned above. Similarly, Gambell and Mestorff (1964) working with whiting, Merlangius merlangus, considered the nuclear edge to reflect

FIGURE 6. Total length: otolith radius regressions and correspondence of annuli (r1 - r4) in (a) male and (b) female G. vulgaris. Vertical bars denote the 95% confidence intervals of the mean values of each annulus radius in each 10 mm TL group. (The confidence limits for the fourth annulus in male G. vulgaris are 47.98 and 52.18 (100 - 110 group), and 40.65 and 64.54 (110 - 120 group)). See text of section 1. for explanation.


a. Males
0·75
0·5
$\bar{R} = 0{\cdot}511\bar{L} - 0{\cdot}3002$
r4, n=6
r3, n=34
r2, n=84
r1, n=152
b. Females
0·75
0·5
$\bar{R} = 0{\cdot}451\bar{L} + 3{\cdot}5997$
r4, n=13
r3, n=48
r2, n=123
r1, n=202
30
50
70
90
110
130
Otolith Ring Radius in mm
Total Length in mm

a change from pelagic to benthic habits rather than an indicator of age.

The sagittal otolith of one side of the head was the mirror-image of that on the other side in all fish examined, except two, in both of which one otolith was normal and the other was underdeveloped. In one instance the nucleus was normally developed, but the rest of the otolith was extremely thin and transparent. In the other instance the abnormal otolith, although showing annuli, was of a more hyaline nature than is normal. It has been shown that inorganic material, chiefly in the form of aragonite, is laid down throughout the otolith, whilst organic material is restricted to the more opaque parts (Irie, 1955; Dannevig, 1956; Mina, 1968; Degens, Deuser and Haedrick, 1969). It would appear that in the two abnormal otoliths there was a breakdown in the processes concerned with the deposition of organic material.

Although both otoliths were generally similar, to standardize procedure all measurements were made on the flat side of the left otolith.

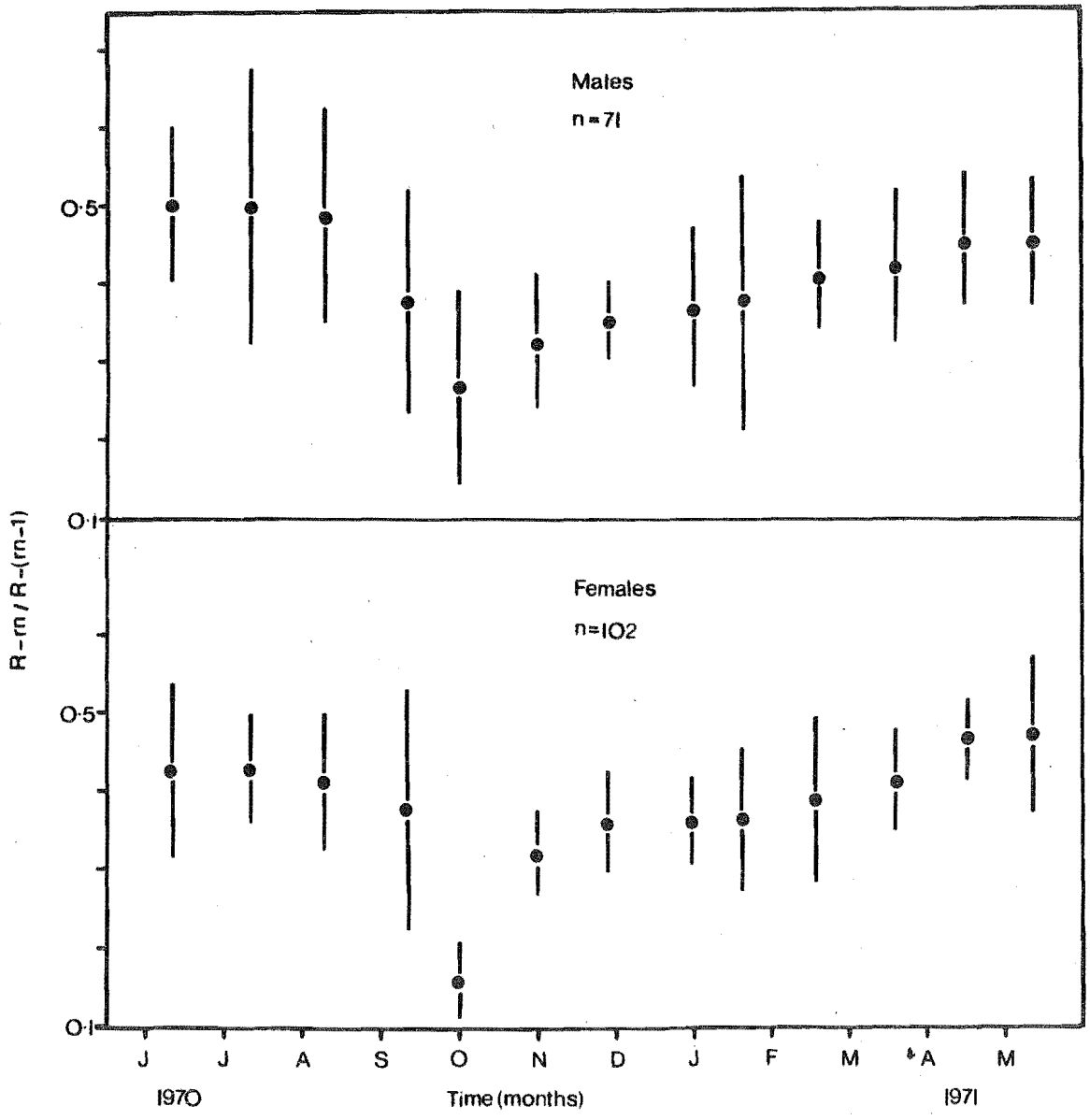
(b) Validation of the otolith method

In order that annuli could be used to age G. vulgaris it was necessary to show that they were formed at regular time intervals.

The pattern of annulus formation was examined by considering the relationship between the radius of each annulus and the total length of the fish over a period of one year, as described by Matsuura (1961), Mio (1961) and Yunokawa (1961). The otolith radius (R) and the radius of each annulus (r_n) were measured from the centre of the nucleus along the dorso-ventral axis (see Fig. 5) using a micrometer eye piece. Each r_n was measured to the point where the annulus abutted the opaque zone. The r_n measurements were then standardized to adjust for individual variation in growth by multiplying by the factor $\bar{R}/R$, where $\bar{R}$ was the mean otolith radius for any observed total length. $\bar{R}$ was determined separately for males (252 fish) and females (293 fish) from the relationship between total length and otolith radius. This relationship is indicated by the diagonal regression lines in Fig. 6a, b.

(The total length:otolith radius regressions for males and females were compared by means of analysis of covariance (Snedecor and Cochran, 1967) after Bartlett's test of homogeneity of variances

FIGURE 7. Time of annulus formation in the otoliths of *G. vulgaris* as indicated by changes in the marginal growth index. The mean value for each index is given together with its 95% confidence intervals (vertical bars).


Males
n=71
Females
n=102
R-rn / R-(rn-1)
0·5
0·1
0·5
0·1
J
J
A
S
O
N
D
J
F
M
A
M
1970
Time (months)
1971

(Sokal and Rohlf, 1969) indicated that the test was valid ($\chi^2 = 0.4769$, d.f. = 1). Analysis of covariance indicated that although there was no significant difference ($P>0.01$) between intercepts ($F = 1.1603$, d.f. = 1 and 542), there was a significant difference ($P<0.01$) between slopes ($F = 16.4223$, d.f. = 1 and 541). This indicated that the rate of deposition of otolith material was different for males and females. Therefore, all subsequent analyses were carried out separately for the two sexes.)

The mean values of standardized annulus radii ($\bar{r}_n$) were then determined for a subsample of fish in each 10 mm length class and are given with 95% confidence intervals in Fig. 6a, b. It may be seen in Fig. 6a, b, that straight lines can be drawn parallel to the total length axis through each annulus radius, showing that equivalent annuli occur in the same position in the otolith irrespective of both the total length of the fish and the number of annuli in the otolith. For example, the position of annulus 1 in a 2-annulus otolith from the 70–80 mm length class is similar to that of annulus 1 in a 4-annulus otolith from the 120–130 mm length class. Such correspondence of annuli indicates the regular temporal pattern in which they were formed.

Although it has been assumed by a number of workers that annuli are formed once a year, this is not always the case (e.g. Yunokawa, 1961). The time of annulus formation in G. vulgaris was estimated from the monthly changes in marginal growth index of the otolith (Matsuura, 1961; Mio, 1961; Yunokawa, 1961; Staples, 1971). The growth index is given by the formula:

$$G_I = \frac{R - r_n}{R - r_{n-1}}$$

where G_I is the marginal growth index, R is the total otolith radius and r_n and r_{n-1} are the radii of the ultimate and penultimate annuli, respectively. All measurements were made to the outer edge of each annulus where it abutted the next outer opaque zone. The mean marginal growth index was determined monthly for fish of each sex. The indices from June 1970 to May 1971 are presented in Fig. 7a, b, together with their 95% confidence intervals. As shown by the sharp decrease in the growth index, the annulus formed in the otolith from August to October.

Within this period the exact time of formation varied between fish and 1st October was chosen arbitrarily as the date of annulus formation. Therefore, it is apparent that one annulus was formed during the year, in winter and early spring, and one opaque zone was laid down in late spring, summer and autumn.

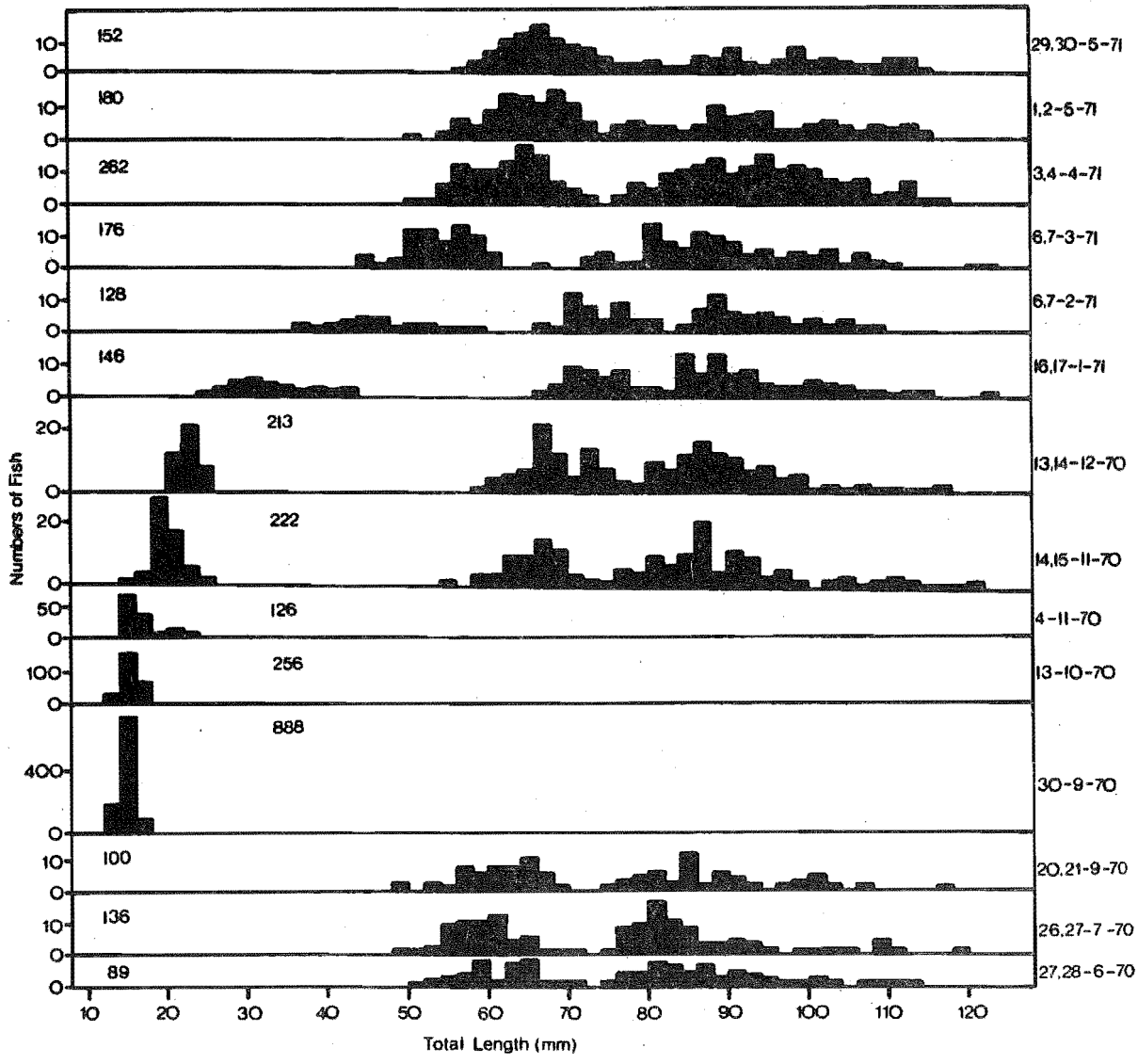
Thus, fish in their first year of life with no annulus formed were designated by international convention as age 0+ (see Tesch, 1968). The first annulus was formed by the following October, approximately one year after hatching (which extended from late September to November - see Chapter IV). After formation of the first annulus, fish entered their second growing season and were designated age 1+, and so on.

(c) Factors affecting the formation of annuli

A number of workers have indicated a correlation between the time of annulus formation and certain external parameters, e.g. temperature (Jensen, 1957; Ouchi, 1969) and food (Bhatia, 1931a, b, 1932). Hartley (1947) considered annuli to be spawning marks, whilst Brown (1946a), van Someren (1950b) and Holden (1955) thought that condition or some internal cycle played a major role. Even though experiments such as those of Bhatia and Ouchi (loc. cit.) indicate that certain external factors play an important role in some species, it is difficult to isolate the particular factor(s) which is/are directly responsible for annulus formation (De Bont, 1967). Recently, Pannella (1971) has demonstrated the occurrence of daily growth in the sagittae of all the species he has studied. He suggested that there is a relation between the rate of calcification and reproduction.

Annulus formation in G. vulgaris occurred during late winter and early spring at a time when day length and water temperature were increasing and when growth rate was at a minimum (see section 2 of this Chapter). This coincided with the breeding season. However, annuli formed at the same time in young-of-the-year fish irrespective of whether or not they spawned. Thus, all young-of-the-year females formed annuli although none of them shed eggs or were even ripe, and all young-of-the-year males formed annuli although some of them did not spawn (see Chapter IV). Therefore, spawning as such was not

FIGURE 8. Length frequency distributions of G. vulgaris from June 1970 to May 1971. From September to December, samples of recently-hatched fish were obtained from quiet stretches of the River Glentui immediately below the riffles in which the adults were found; from January onwards all fish were sampled in riffle areas.


152
29,30-5-71
180
1,2-5-71
262
3,4-4-71
176
6,7-3-71
128
6,7-2-71
146
16,17-1-71
213
13,14-12-70
222
14,15-11-70
126
4-11-70
256
13-10-70
888
30-9-70
100
20,21-9-70
136
26,27-7-70
89
27,28-6-70
Numbers of Fish
Total Length (mm)

responsible for annulus formation, at least in young-of-the-year fish. At the same time of the year there was a reduction in the condition of fish (see section 3 of this Chapter). This occurred not only because of the decrease in gonad weight in those fish which spawned, but also because of the depletion of fat reserves which were at a minimum in August and September. During the same period there was a reversal of the diel activity cycle (Chapter VI) and a change in the normal sedentary habits of the fish (see Chapter V). It was therefore a time of physiological readjustment.

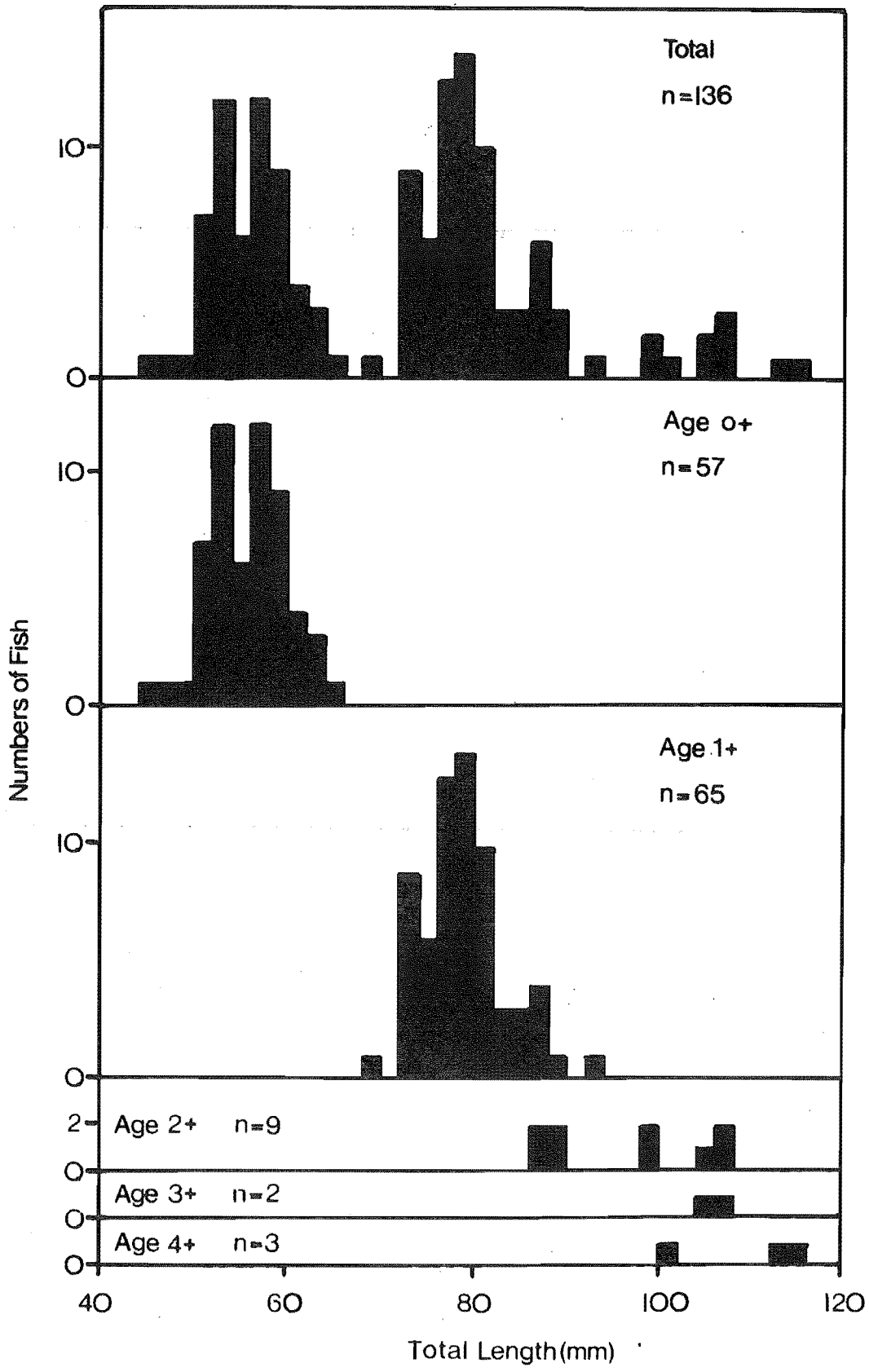
As Nikolsky (1963) pointed out, it would be incorrect to assume that annulus formation occurred merely as a response to changes in growth or metabolism brought about by altered external conditions. He concluded that annulus formation depended on a number of simultaneous processes affected by both internal and external factors. Similarly, in G. vulgaris annulus formation appears to depend on a physiological mechanism affected by factors both internal and external. Experimental analysis is required to indicate those factors which most affect this mechanism and thereby control the time of formation of annuli.

(2) Length frequency analysis

Length frequency analysis may be used to age fish which have a relatively limited spawning season. At any one time a population of such fish consists of a series of discrete age groups. The size range of each age group tends to be distinct from that of adjacent groups and may be indicated by a mode in a length frequency distribution. This method of ageing is applicable to G. vulgaris which has one well-defined spawning season in late winter and early spring (see Chapter IV).

The number of fish in each 2 mm length class was recorded for each regular monthly sample and for samples of recently-hatched fish. The resulting polymodal length frequency distributions from June 1970 to May 1971 are presented in Fig. 8, (1970 August and October samples are omitted because of small sample sizes). In most months two, and in some months three, distinct length groups are indicated, but for most of the year only the first two groups can be separated by this method. Since the whole population was represented in the above samples, the first group represents fish in their first year of life, designated age 0+, the next group represents fish in their second year

FIGURE 9. Length frequency distribution of G. vulgaris in the River Glentui in July 1970, together with the length frequency distributions of the component age groups as determined from otoliths.


Total
n=136
Age 0+
n=57
Age 1+
n=65
Age 2+ n=9
Age 3+ n=2
Age 4+ n=3
Numbers of Fish
Total Length (mm)
10
0
2
40
60
80
100
120

of life, designated age 1+, and so on.

For a comparison of the otolith and length frequency methods, the age of each fish in the July 1970 sample was determined from otoliths. The length frequency distribution of fish in each age group was then plotted and is given in Fig. 9, together with the total length frequency distribution for that month. It can be seen that fish designated 0+ and 1+ by both methods coincide. This further validates the use of otoliths for ageing G. vulgaris.

The method of length frequency analysis is inadequate for ageing older fish, mainly because of the low numbers surviving for more than three years. There is also an increasing overlap in the length frequency distributions of older fish produced by individual variation and reduced growth rate. The situation is further complicated by different rates of growth in males and females after the first year of life (see section 2 of this Chapter). This is indicated by the bimodal nature of the second (age 1+) and third (age 2+) length classes in most months and is shown particularly well in the December 1970, and the January and February 1971 length frequency distributions (Fig. 8).

In practice, smaller fish were aged by length frequency analysis, while larger fish were aged by reading otoliths.

Most G. vulgaris caught during the present study belonged to the age groups 0+, 1+ and 2+; a few were in the 3+ and 4+ age groups, in their fourth and fifth years respectively; none were found in the 5+ age group, and one was found in the 6+ age group, in its seventh year.

2. Growth

(1) Annual growth in length

Data on annual growth in length of G. vulgaris were derived by back-calculation from otoliths using the formula given by Rounsefell and Everhart (1953) and Nikolsky (1963):

$$L_n = \frac{R_n}{R}(L - c) + c \qquad (1)$$

where L_n is the length of the fish at age n (i.e. when the nth ring was formed), L is the length of the fish and R is the otolith radius when the sample was taken, R_n is the radius of ring n, and c is the hypothetical

length of the fish at the moment the otolith began to form. The value of c is derived by extrapolation from the total length-otolith radius regression (Fig. 6a, b) and is the intercept on the total length axis; for males c = 0.56 and for females c = -8.08. For fish aged from one to four years, mean back-calculated lengths together with their 95% confidence limits are presented in Table 3.

TABLE 3. Mean, annual, back-calculated lengths of G. vulgaris derived from otoliths, together with their 95% confidence limits (CL). (TL = total length).

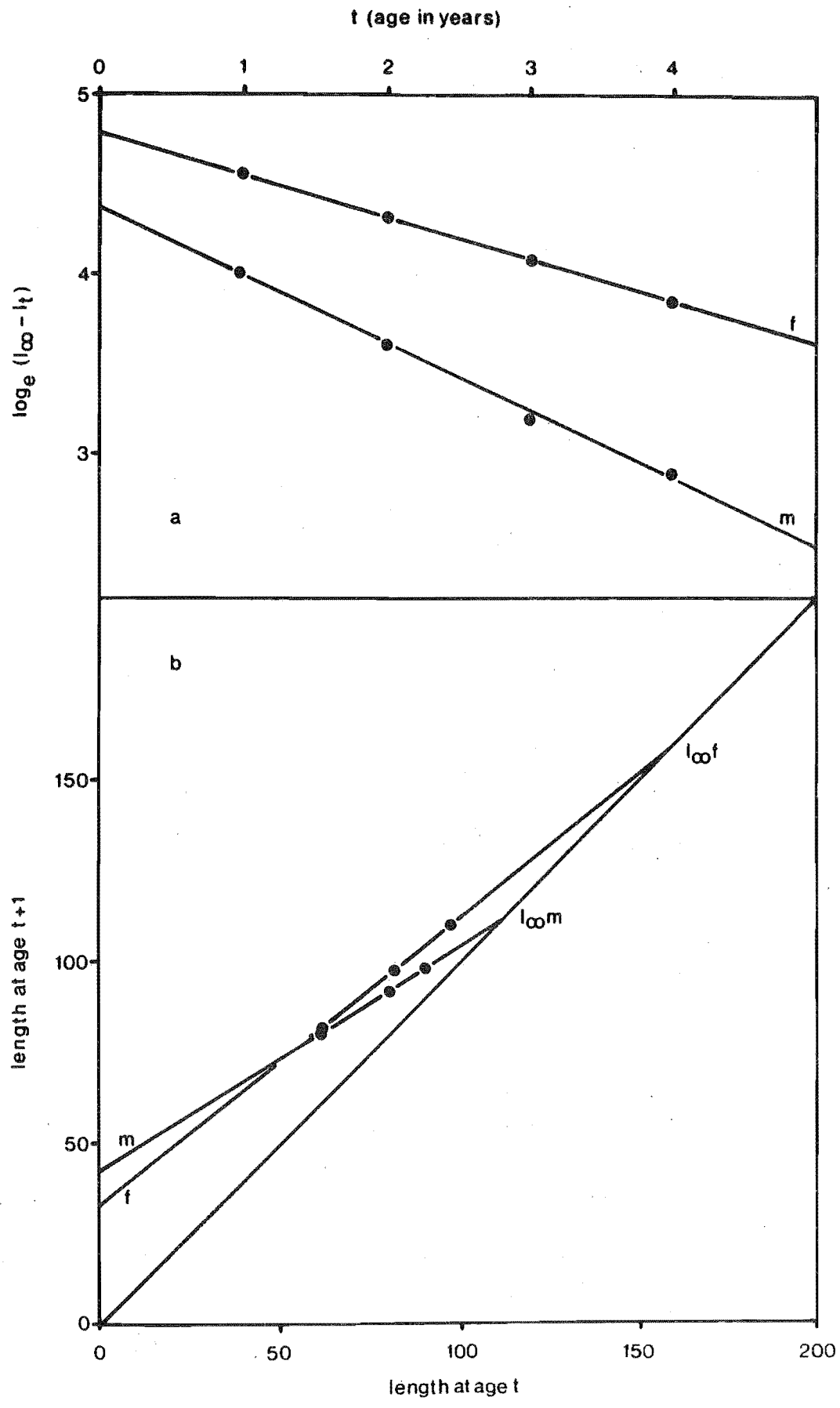
	Males			Females		
Age	Mean TL (mm)	95% CL	Sample size	Mean TL (mm)	95% CL	Sample size
1	61.33	0.7156	157	61.66	0.7307	208
2	79.06	1.2872	85	81.52	1.0791	122
3	91.12	1.9425	32	97.45	1.8622	45
4	97.81	4.3493	8	110.07	3.8940	14

Back-calculated mean lengths showed no evidence of Lee's phenomenon, i.e. the tendency for calculated lengths at a given age to be smaller, the older the fish from which they are calculated (Lee, 1912; Hile, 1936; Tesch, 1968).

Length achieved at the end of the first year of life was not significantly different ($P > 0.05$) between males and females ($t = 0.6351$, d.f. = 363). However, after the first year, growth in length of males lagged behind that of females. Student's t-tests, used to compare the mean lengths achieved at the end of the second, third and fourth years of life, showed highly significant ($P < 0.01$) differences between males and females, ($t = 2.9068$, d.f. = 205; $t = 4.7828$, d.f. = 75; $t = 4.7572$, d.f. = 20 for comparison of lengths achieved at the end of the second, third and fourth years of life respectively).

The von Bertalanffy equation (von Bertalanffy, 1938) was used to describe annual growth in length of G. vulgaris; it is

FIGURE 10. Graphical estimation of the constants of the von Bertalanffy equation, (m = males, f = females). See text of section 2.(1) for explanation.


t (age in years)
0
1
2
3
4
5
4
3
$\log_e (l_\infty - l_t)$
f
m
a
b
$l_\infty f$
$l_\infty m$
150
100
50
0
m
f
length at age t+1
0
50
100
150
200
length at age t

represented by:

$$l_t = l_\infty(1 - e^{-K(t - t_o)}) \qquad (2)$$

where l_t is the length at age t, l_∞ is the average "maximum" or asymptotic length, K is a constant determining the rate of change in the length increment, t is age in years and t_o is the hypothetical age when length is zero. This equation has been widely used in fisheries investigations (see, for example, Kohler, 1959; Pantulu, 1962; May, Pinhorn, Wells and Fleming, 1965; Cieglewicz, Dragonik and Zubowski, 1969; Halliday, 1969) and methods of fitting it have been described by Beverton and Holt (1957), Ricker (1958) and Allen (1966). However, the growth of all fish species is not represented satisfactorily by the equation (Allen, 1969b) and a number of other growth models is to be found in the literature (see Dickie, 1968; Rafail, 1971). The physiological basis of the von Bertalanffy equation has been attacked by a number of workers (e.g. Ricker, 1958; Hemmingsen, 1960) and the concept of asymptotic growth has been questioned by Larkin, Terpenning and Parker (1957), Paloheimo and Dickie (1965) and Knight (1968). Also, Silliman (1969), showed that for some species in which the von Bertalanffy equation adequately describes growth, an asymptote has no biological meaning. For example, in chum salmon, Oncorhynchus keta, the asymptote would not be approached until several years beyond the maximum age of the species, since all chum salmon die after spawning at or before five years of age. However, while the biological interpretation of growth models and their parameters still presents problems (Dickie, loc. cit.) there is no doubt of the general value of expressions such as the von Bertalanffy equation for descriptive purposes.

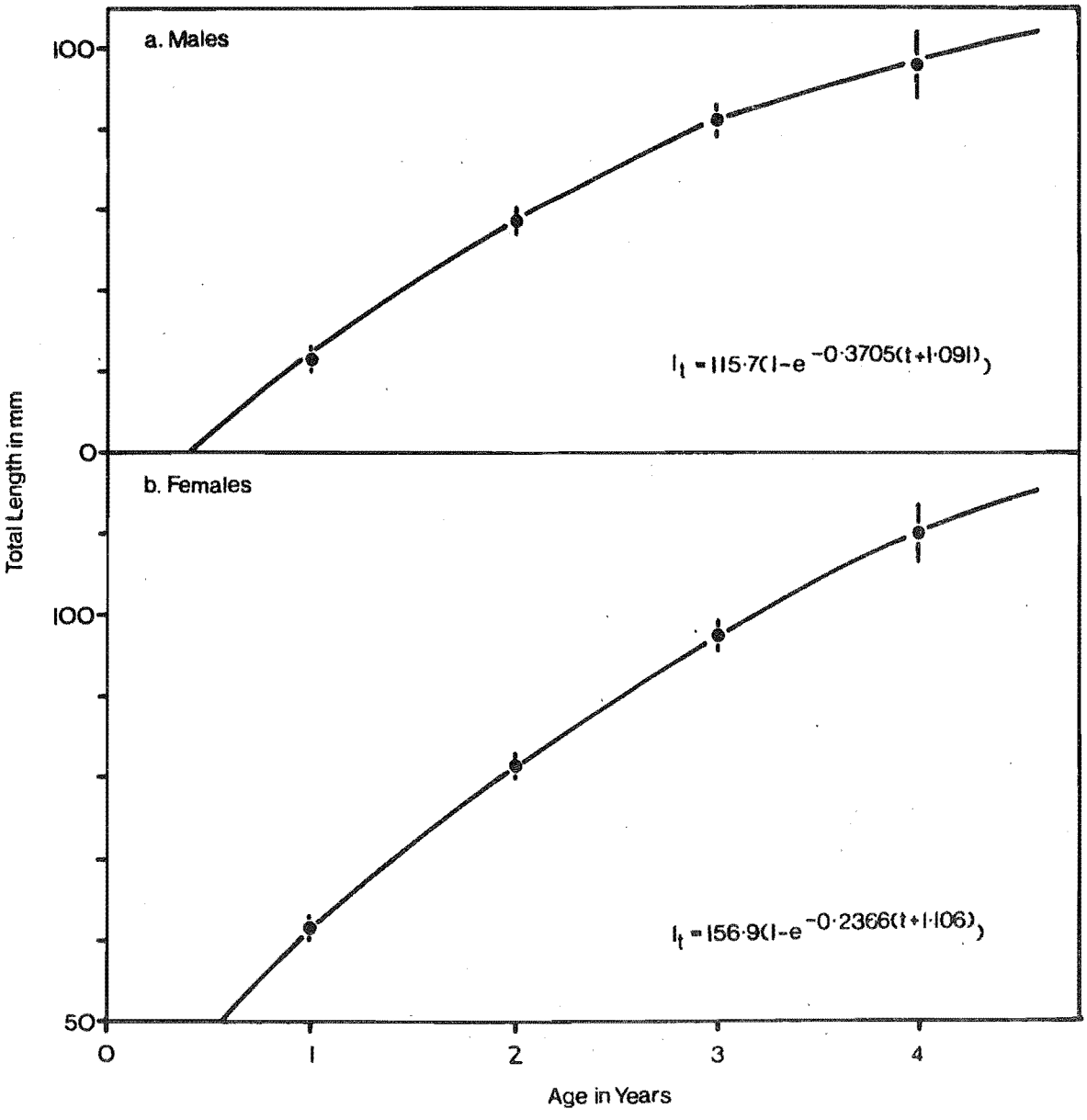
In the present study the equation was fitted using the procedure described by Beverton and Holt (1957) and Ricker (1958).

Firstly l_∞ was calculated for males and females using the expression developed by Ford (1933) and Walford (1946), viz.

$$l_{t+1} = l_\infty(1 - k) + kl_t \qquad (3)$$

Fitted Walford graphs (see Fig. 10b) of l_{t+1} (length at age t + 1) against

FIGURE 11. Annual growth in length of *G. vulgaris*. The mean total length of each age group, together with its 95% confidence interval (see Table 3), is superimposed on the fitted von Bertalanffy growth curve.


a. Males
100
0
$l_t = 115{\cdot}7(1-e^{-0{\cdot}3705(t+1{\cdot}091)})$
b. Females
100
50
$l_t = 156{\cdot}9(1-e^{-0{\cdot}2366(t+1{\cdot}106)})$
0
1
2
3
4
Age in Years
Total Length in mm

l_t (length at age t) yielded values for k (slope) of 0.63 and 0.8 for males and females respectively. The intercepts (males = 42.8, females = 31.38) were equated to $l_\infty(1 - k)$ and thus values of l_∞ were calculated, giving 115.7 for males and 156.9 for females.

Secondly, K and t_o were calculated using the natural logarithmic form of equation (2), viz.

$$\log_e (l_\infty - l_t) = \log_e l_\infty + Kt_o - Kt \qquad (4)$$

The fitted graph of $\log_e (l_\infty - l_t)$ against t was a straight line of negative slope (see Fig. 10a) from which K (slope) and the Y-axis intercept were obtained; for males K = 0.3705 and the Y-axis intercept = 4.3471, and for females K = 0.2366 and the Y-axis intercept = 4.7941. Values of t_o were calculated by equating the Y-axis intercept to $\log_e l_\infty + Kt_o$; for males $t_o = -1.091$, and for females $t_o = -1.106$.

Thus the von Bertalanffy equation describing growth in length of males was found to be:

$$l_t = 115.7\,(1 - e^{-0.3705(t + 1.091)})$$

and for females:

$$l_t = 156.9\,(1 - e^{-0.2366(t + 1.106)})$$

The fitted curves are presented in Fig. 11a, b, together with the empirically determined values of mean length at each age (see Table 3); 95% confidence intervals for each mean length are also included. It may be seen in Fig. 11a, b that the von Bertalanffy equation adequately describes growth in length of males and females of G. vulgaris over the first four years of life.

(2) Seasonal growth in length

Seasonal growth in length was estimated from monthly changes in the mean length of each age group. Mean lengths were calculated directly from groups of recently-hatched fish where there was no overlap in length distribution with older age groups. For other groups in the regular monthly samples mean lengths were estimated from length frequency distributions using the probability paper method (Buchanan-Wollaston and Hodgson, 1929; Harding, 1949; Cassie, 1950, 1954;

TABLE 4. Mean lengths (mm) (+ one standard deviation in parenthesis) of G. vulgaris in the River Glentui, from June 1970 to May 1971. Age 0+ fish have been included as males.

	1970							1971			
	June 27–28	July 26–27	Sept. 20–21	Nov. 14–15	Dec. 13–14	Jan. 16–17	Feb. 6–7	March 6–7	April 3–4	May 1–2	May 29–30
Males & Females 0+			11.3[a] (0.8) 12.1[b] (1.5)	13.3[c] (2.4) 16.3[d] (1.7)	19.2 (2.4)	29.9 (4.7)	43.2 (5.7)	51.4 (4.2)	59.7 (5.1)	61.6 (5.1)	63.5 (4.9)
Males 0+/1+	57.8 (4.6)	56.3 (4.2)	58.3 (4.6)	61.4 (3.1)	62.8 (3.5)	67.7 (2.1)	67.5 (1.5)	70.6 (1.5)	75.4 (0.8)	76.0 (2.4)	76.8 (1.3)
Females 0+/1+					68.6 (2.6)	73.4 (1.6)	73.8 (1.8)	77.9 (1.6)	82.6 (3.6)	85.4 (2.1)	85.3 (3.8)
Males 1+/2+	76.6 (2.6)	77.6 (2.9)	75.6 (2.8)	76.3 (3.3)	77.4 (1.0)	81.0 (1.8)	84.7 (1.9)	84.7 (1.5)	90.3 (1.8)	90.7 (1.0)	94.6 (3.0)
Females 1+/2+	82.8 (1.0)	81.6 (4.7)	83.1 (1.4)	82.2 (1.4)	84.0 (2.5)	85.4 (0.7)	91.1 (1.6)	90.9 (1.2)	95.8 (1.9)	98.2 (3.4)	100.5 (1.7)

a, b, c, d = samples taken on 30–9–70, 13–10–70, 4–11–70 and 20–11–70 respectively

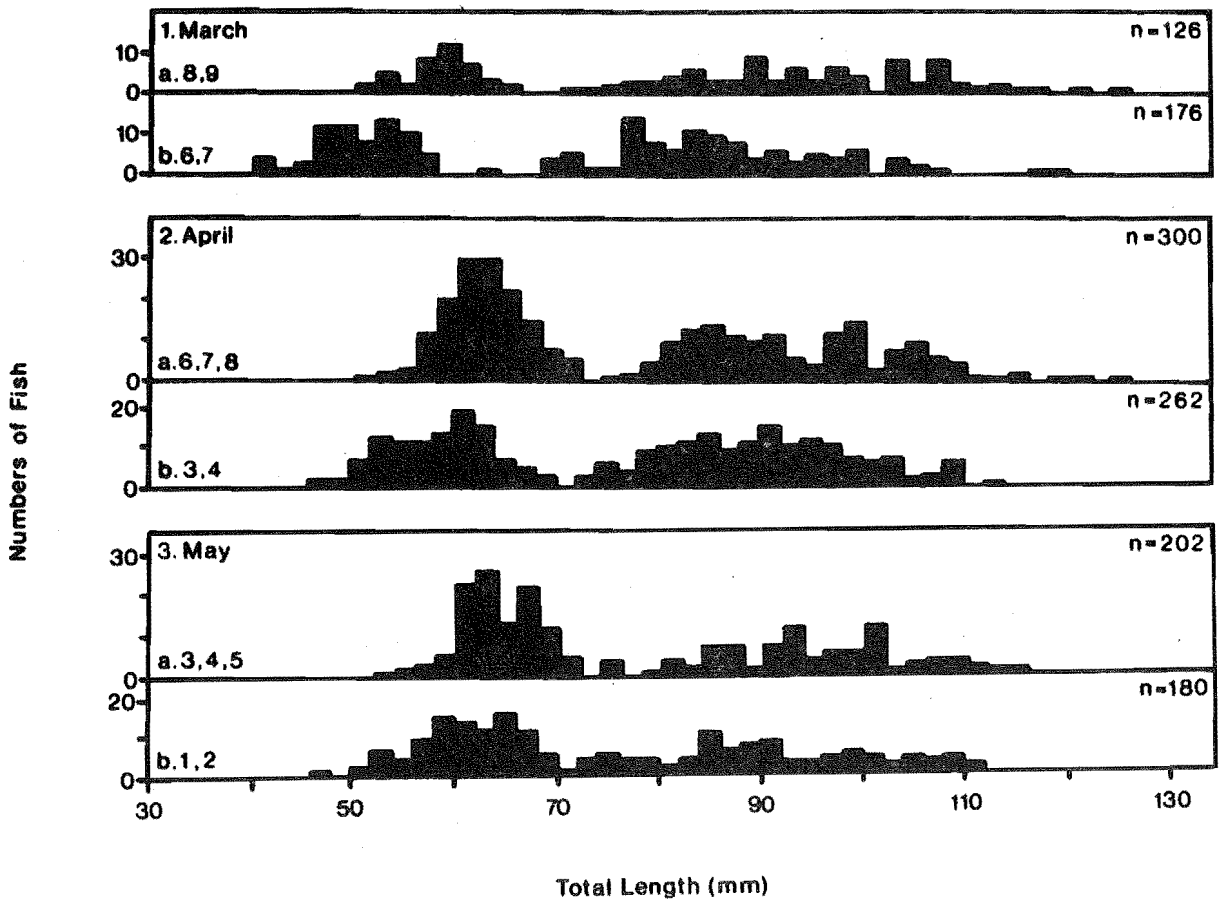
FIGURE 12. Length frequency distributions of samples of *G. vulgaris* taken in different parts of the River Glentui in 1971.

Key to letters:

a. Samples taken during the home range investigation from section e - f (see Fig. 1).

b. Samples taken during the regular sampling programme from section c - d (see Fig. 1).

(n = sample size).


1. March
n=126
a. 8,9
n=176
b. 6,7
2. April
n=300
a. 6,7,8
n=262
b. 3,4
3. May
n=202
a. 3,4,5
n=180
b. 1,2
10
0
30
20
30
50
70
90
110
130
Numbers of Fish
Total Length (mm)

Harris, 1968). This method was used to measure seasonal growth in fish up to age 2+; the small numbers in the population did not permit the use of this method to follow seasonal growth in older fish. Mean lengths of G. vulgaris from June 1970 to May 1971 are presented in Table 4.

The period of increase in length for both males and females extended from November through to the following May, with maximum growth occurring from December to April. Growth ceased from June to October, in winter and early spring. Benzie (1968d) found a similar pattern of growth in length in young-of-the-year G. vulgaris in another Canterbury river (the Cass River), where fish reached a mean length of 58.6 mm* in their first year of life with no significant growth occurring between June and September.

Differences in growth in length between year classes were apparent, e.g. in the May (29-30) 1971 sample, age 0+ fish had reached a length of 63.5 mm, whereas in the June 1970 sample, 0+ fish had attained a length of only 57.8 mm.

Seasonal growth in length also varied in different parts of the River Glentui. This was indicated by comparing the length frequency distributions of fish caught at the same time in different parts of the River. Figure 12 shows the length frequency distributions of the regular samples taken in March, April and May 1971, together with samples taken during the same periods from further downstream, as part of the home range investigation (see Chapter V). The greatest differences were those between age 0+ fish; mean lengths of this age group together with the differences between samples are presented in Table 5. Different rates of growth in fish of the same species in different parts of the same river have been reported also by Went and Frost (1942) and Purkett (1958).

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* Benzie's data were converted from standard lengths to total lengths using a conversion factor of 1.149 (derived from the ratio between these two measurements in G. vulgaris given by McDowall (1970)).

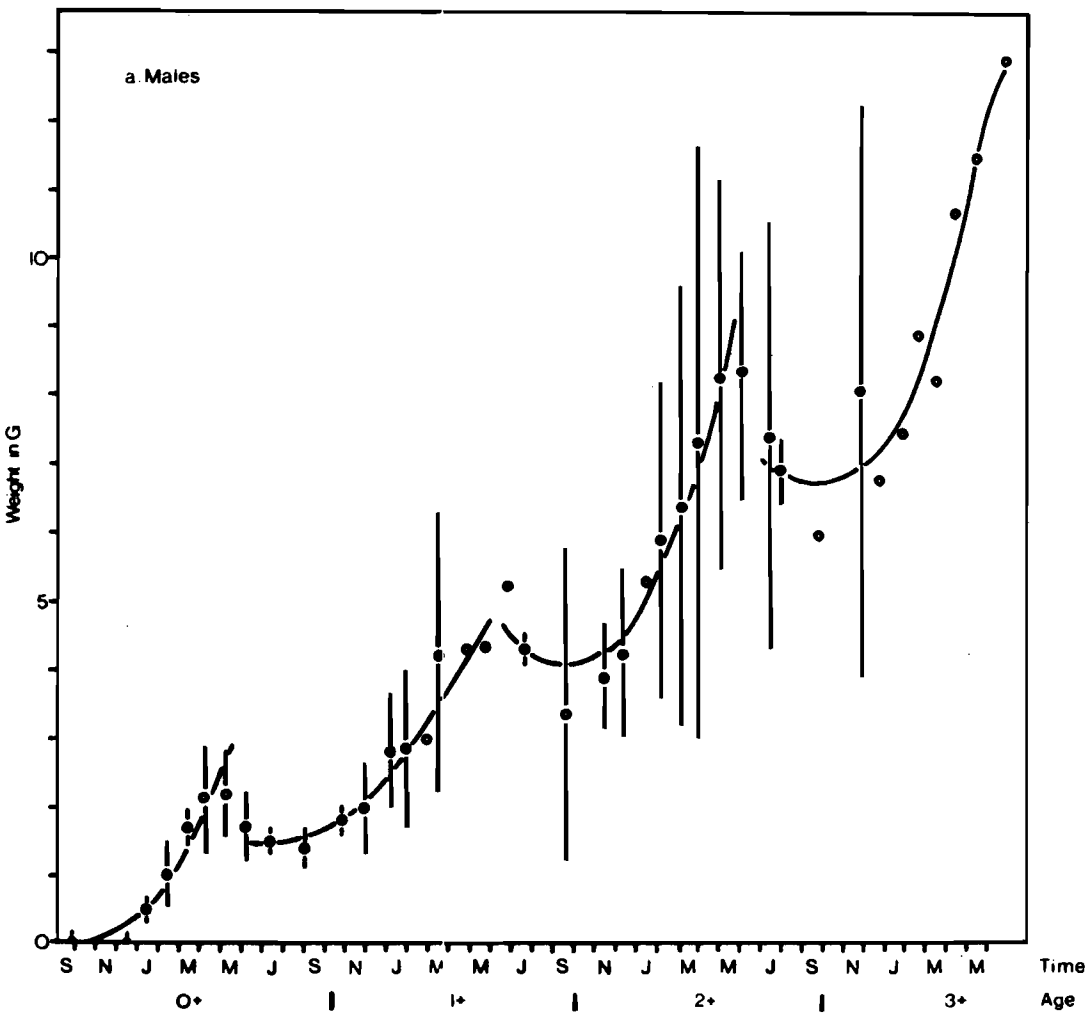

a. Males
Weight in G
0
5
10
S N J M M J S N J M M J S N J M M J S N J M M
Time
0+
1+
2+
3+
Age

FIGURE 13. Seasonal growth in weight of G. vulgaris. Curves are 2nd degree polynomials except in the case of age 0+/1+ females (5th) and age 1+/2+ females (7th). Each curve represents the smallest polynomial which gives a 5% fit to the data. 95% confidence intervals of mean wet weights are indicated by vertical bars; o indicates that the mean was derived from a sample of less than five fish.

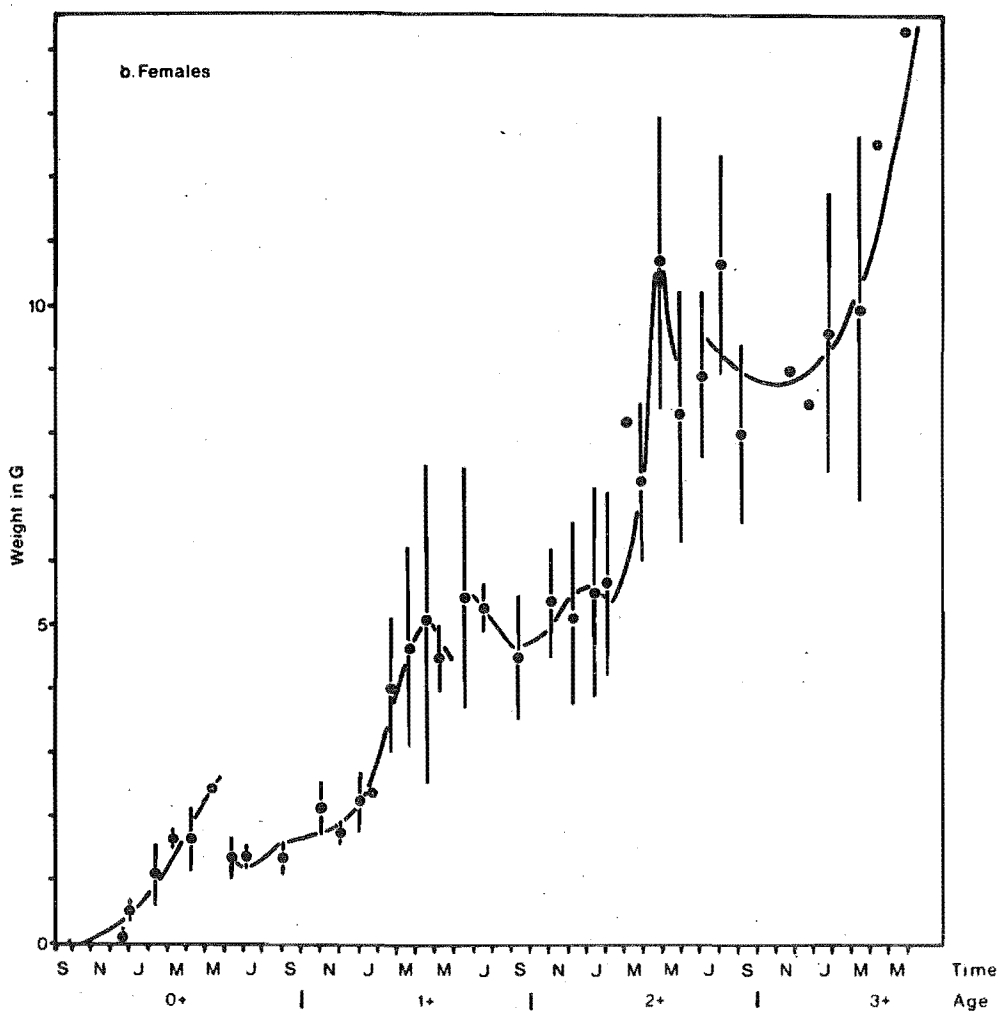

b. Females
Weight in G
0
5
10
S N J M M J S N J M M J S N J M M J S N J M M
Time
0+
1+
2+
3+
Age

TABLE 5. Mean lengths (mm) (with one standard deviation in parenthesis) of age 0+ G. vulgaris caught during the same periods in different parts of the River Glentui. The difference between paired means in each instance is significant at the 0.001 level.

Regular samples:	March 6, 7	April 3, 4	May 1, 2
	51.4 (4.2)	59.7 (5.1)	61.6 (5.1)
Home range samples:	March 8, 9	April, 6, 7, 8	May 3, 4, 5
	59.2 (3.5)	63.5 (4.0)	65.4 (4.2)
Difference between means:	7.8	3.8	3.8
t	10.579	6.433	5.797
d.f.	107	254	206

(3) Seasonal growth in weight

Mean wet weights of each age group were obtained from fish sub-sampled from regular monthly samples. Growth curves, fitted by the method of successive polynomials, described growth in weight of fish in the younger age groups; older fish were present in insufficient numbers to provide adequate data on growth in weight. Growth curves describing growth in weight of males and females of the younger age groups from June 1970 to May 1971 are presented in Fig. 13. The largest G. vulgaris caught in the present study was an age 4+ female which weighed 20.9 g and was 125 mm long; the largest male also was aged 4+ and weighed 13.5 g and was 107 mm long.

(4) Factors affecting growth

Growth results from the consumption of food, its assimilation, and its transformation into body constituents. As indicated by Coche (1967) it may be regarded as the energy surplus transformed to tissue after the metabolic requirements for maintenance have been met. Thus, any factor which affects either directly or indirectly the consumption and assimilation of food and its transformation into tissue may be regarded as having an effect on growth.

The importance of both the quantity and quality of food in affecting

the growth of fish has been demonstrated in a number of experimental situations (e.g. Pentelew, 1939; Brown, 1957; Paloheimo and Dickie, 1965, 1966a, b; Warren and Davis, 1967); such studies have been used to provide an indirect estimate of food consumption under natural conditions. However, it is difficult to demonstrate the importance of food availability as a factor influencing growth under natural conditions unless detailed information is available on the feeding behaviour of the fish and on the relative abundance and accessibility of the prey. At no time during the present investigation did the abundance of prey species appear to be a limiting factor. Since G. vulgaris is basically a drift-feeder the availability of its prey depends on those factors responsible for causing drift (see Chapter VI). The percent occurrence of empty stomachs in samples of G. vulgaris was generally low from October to March, when most growth occurred. Although a number of factors are involved in the interpretation of this observation (see Chapter VI), it appears that during these months more food was consumed than at other times of the year.

The effect of temperature on metabolism, food intake and growth has been demonstrated by a number of workers (e.g. Markus, 1932; Brown, 1946b; Baldwin, 1956; Frost and Kipling, 1968; Elwood and Waters, 1969; McCormick, Hokansen and Jones, 1972) and under natural conditions changes in growth rate have often been correlated with changes in temperature (Swift, 1961; Nikolsky, 1963; May, Pinhorn, Wells and Fleming, 1965; Frost and Kipling, 1967; Muth, 1969; Johnson, 1970). In G. vulgaris most growth occurred in the months when the highest water temperatures were recorded (see Fig. 3b), while growth ceased in those months when water temperatures were low. The importance of the influence of temperature on the length of the growing season was pointed out by Van Oosten (1944). In G. vulgaris, temperature appeared to affect the length of the growing season particularly for young-of-the-year fish, in that higher temperatures were correlated with earlier spawnings (see Chapter IV) so that those fish which hatched from early spawnings had a longer growing season than those hatched from late spawnings. The onset of spawning differed by up to six weeks in different parts of the River (see Chapter IV) so that

differences in length frequency distributions from different parts of the River (Fig. 12) were to be expected.

The seasonal growth cycle may be influenced by light acting through changes in daylength. This was suggested by Johnson (1966) who, working under laboratory conditions simulating those in nature, found that there were seasonal changes in both growth and maintenance requirements of pike, Esox lucius, which were to some extent independent of temperature. Gross, Roelofs and Fromm (1965), working with green sunfish, Lepomis cyanellus, showed that photoperiod had a marked effect on food consumption, food conversion efficiency and growth; growth rates were highest in regimes of increasing photoperiod and lowest in regimes of decreasing photoperiod. They suggested that photoperiod influenced growth by increasing conversion efficiency and also possibly through stimulating food consumption. However, Stickney and Andrews (1971) found that photoperiod had no substantial influence on the growth rate or food conversion of channel catfish, Ictalurus punctatus. G. vulgaris is generally nocturnal and obtains most of its food at night (see Chapter VI). However, maximum growth occurred at a time when nights were shortest and consequently the potential time for food consumption was reduced.

A number of workers (e.g. Hile, 1936; Frost and Kipling, 1967; Staples, 1971 unpublished), have shown an inverse relationship between population density and growth rate (see also Weatherley, 1972). This is normally explained by different degrees of intraspecific competition for food. Thus, at high density, competition is severe and individual growth rate is reduced. Staples (loc. cit.), working with Philypnodon breviceps, showed that feeding periodicity, food habits and habitat preferences differed between age groups and thus competition for food was more important with respect to growth within an age group rather than between age groups. Various interspecific relationships may also affect the rate of growth (see Nilsson, 1967b; Weatherley, 1972).

Brown (1957), Ivlev (1961), Chen and Prowse (1964) and Chen (1965) described experiments in which it was shown that space factors had an effect on growth; both the total volume of water and the degree of crowding of the individuals (acting independently of competition for food) were thought to be important. The latter factor is possibly

significant in the case of recently-hatched G. vulgaris which are gregarious, but is unlikely to have an effect on adult fish which generally lead a solitary existence. In the case of river-dwelling fish, water movement may affect the growth rate (acting independently of the amount of food carried in the drift), maintenance requirements being higher in fast currents than in more sluggish waters. Both volume and movement of water, notwithstanding the character of the river bed, ultimately depend on rainfall. Campbell (1957) suggested that the increased growth rate of Salmo trutta immediately after flooding (in this case by raising the level of a lake) was caused by a temporary increase in the food supply. However, volume and movement of water as such must be considered as factors directly affecting growth rate. The physico-chemical condition of the water may also affect growth (Hile, 1936).

Variation in growth rates between the sexes occurs in many fish (e.g. Hile, 1954; Bodola, 1965). In G. vulgaris the different rates of growth in males and females after the first year of life may be explained, at least in part, by the fact that females do not spawn until the end of their second year of life, whereas many males spawn at the end of their first year (see Chapter IV). Growth in length ceases during the spawning period, but growth in weight is most affected because of shedding of the sexual products (see Fig. 13). In general, growth in length and growth in weight vary together, although detailed studies, such as that of Coche (1967) on steelhead trout, Salmo gairdneri, have shown that significant differences do occur between linear growth and growth in weight.

Thus, growth of G. vulgaris under natural conditions depends on these possible mechanisms, some of which may operate only at certain stages of the life cycle. Experimental analysis is required to determine the relative importance of each factor in determining the growth rate of G. vulgaris.

3. Length:Weight Relationship and Condition

Data on length and weight for each two-monthly period were combined for analysis of the length:weight relationship in G. vulgaris. Males and females were treated separately, and for each sex, fish older than 0+ were lumped together in one group and treated separately

TABLE 6. Results of ANCOVA for comparison of length:weight regressions (of the form log w = a + b log l) between fish aged 0+ and fish aged >0+. (For further explanation see text of section 3).

	Chi square for heterogeneity of variances (d.f. = 1)	Signif. level	F for comparison of slopes	d.f.	Signif. level	F for comparison of intercepts	d.f.	Signif. level
Males								
June, July	43.7772	**	2.7582	1,76	NS	5.7846	1,77	*
Aug., Sept.	0.0124	NS	1.0509	1,37	NS	1.0201	1,38	NS
Oct., Nov.	2.7335	NS	16.7522	1,35	***	0.1279	1,36	NS
Dec., Jan.	0.1118	NS	10.0725	1,31	**	4.6184	1,32	*
Feb., March	2.2628	NS	8.9163	1,32	**	6.0781	1,33	*
April, May	9.9942	**	0.0050	1,71	NS	2.9313	1,72	NS
Females								
June, July	1.6855	NS	3.7438	1,82	NS	7.9857	1,83	**
Aug., Sept.	2.6308	NS	1.2725	1,39	NS	0.9783	1,40	NS
Oct., Nov.	3.8640	*	28.3158	1,45	***	0.4908	1,46	NS
Dec., Jan.	0.9403	NS	14.3070	1,42	***	19.4785	1,43	***
Feb., March	17.5406	**	6.9974	1,37	*	0.1953	1,38	NS
April, May	1.2374	NS	2.7674	1,86	NS	18.4660	1,87	***

NS = Not significant; *, **, *** = significant at the 5%, 1% and 0.1% levels respectively.

TABLE 7. Length (mm): weight (g) relationship of G. vulgaris from June 1970 to May 1971. Relationships are of the form : log w = a + b log l. (n = sample size) (R.H. = recently-hatched fish). (For further explanation see text of section 3).

		Males					Females				
		n	coeff.a	95%CL	coeff.b	95%CL	n	coeff.a	95%CL	coeff.b	95%CL
Age 0+	June, July	38	-5.695	0.015	3.303	0.542	33	-5.063	0.013	2.944	0.511
	Aug., Sept.	24	-4.928	0.019	2.880	0.454	26	-6.013	0.031	3.508	0.675
	Oct., Nov.(R.H)	7+	-5.776	0.060	3.051	1.210	-	-	-	-	-
	Dec., Jan.	13++	-7.452	0.028	4.415**	0.843	-	-	-	-	-
	Feb., March	20	-6.642	0.024	3.895**	0.372	18	-6.177	0.030	3.602*	0.628
	April, May	50	-5.263	0.012	3.109	0.346	62	-4.695	0.011	2.765	0.359
Age>0+	June, July	41	-5.731	0.011	3.333**	0.295	53	-5.798	0.009	3.376**	0.226
	Aug., Sept.	22	-5.637	0.020	3.274	0.508	20	-5.267	0.027	3.084	0.580
	Oct., Nov.	27	-5.771	0.020	3.343**	0.238	39	-5.551	0.017	3.238*	0.205
	Dec., Jan.	22	-5.481	0.022	3.189	0.306	33	-5.637	0.014	3.276**	0.158
	Feb., March	16	-5.507	0.018	3.213	0.301	23	-5.515	0.013	3.230*	0.183
	April, May	25	-5.135	0.011	3.054	0.218	28	-5.475	0.015	3.236	0.253

*, ** = significant deviation from 3.0 at 5% and 1% levels respectively

+ = males and females combined; regression line based on weights of seven samples each of known mean length (total number of fish = 471)

++ = males and females combined; regression line based on weights of 13 samples each of known mean length (total number of fish = 130)

from age 0+ fish. Analysis of covariance (Snedecor and Cochran, 1967) was used to compare regression lines of the form $\log w = a + b \log l$ describing the length:weight relationship of fish aged 0+ and fish older than 0+. The results of these analyses, covering the period from June 1970 to May 1971, are presented in Table 6. Out of twelve analyses the slopes (coefficient b) differed significantly in six cases, whilst the intercepts (coefficient a) differed significantly also in six cases. However, Bartlett's test of homogeneity of variances (Sokal and Rohlf, 1969) indicated that only eight of the twelve comparisons were statistically valid (see the first two columns in the body of Table 6). In spite of this, it was concluded that the length:weight relationships of fish aged 0+ and fish older than 0+ differed sufficiently for subsequent analyses to be carried out separately for the two groups. On this basis, regression lines for the two age groups of each sex were used to describe the length:weight relationship of G. vulgaris for each two-monthly period; regression coefficients (together with their 95% confidence limits) for these relationships are presented in Table 7.

A b coefficient of 3.0 indicates isometric growth and characterizes a fish having an unchanging body form and unchanging specific gravity (Ricker, 1958). Values of b normally range from 2.5 to 3.5 (Carlander, 1969), but regression slopes outside this range may be found at certain stages of growth (McPhee, 1960).

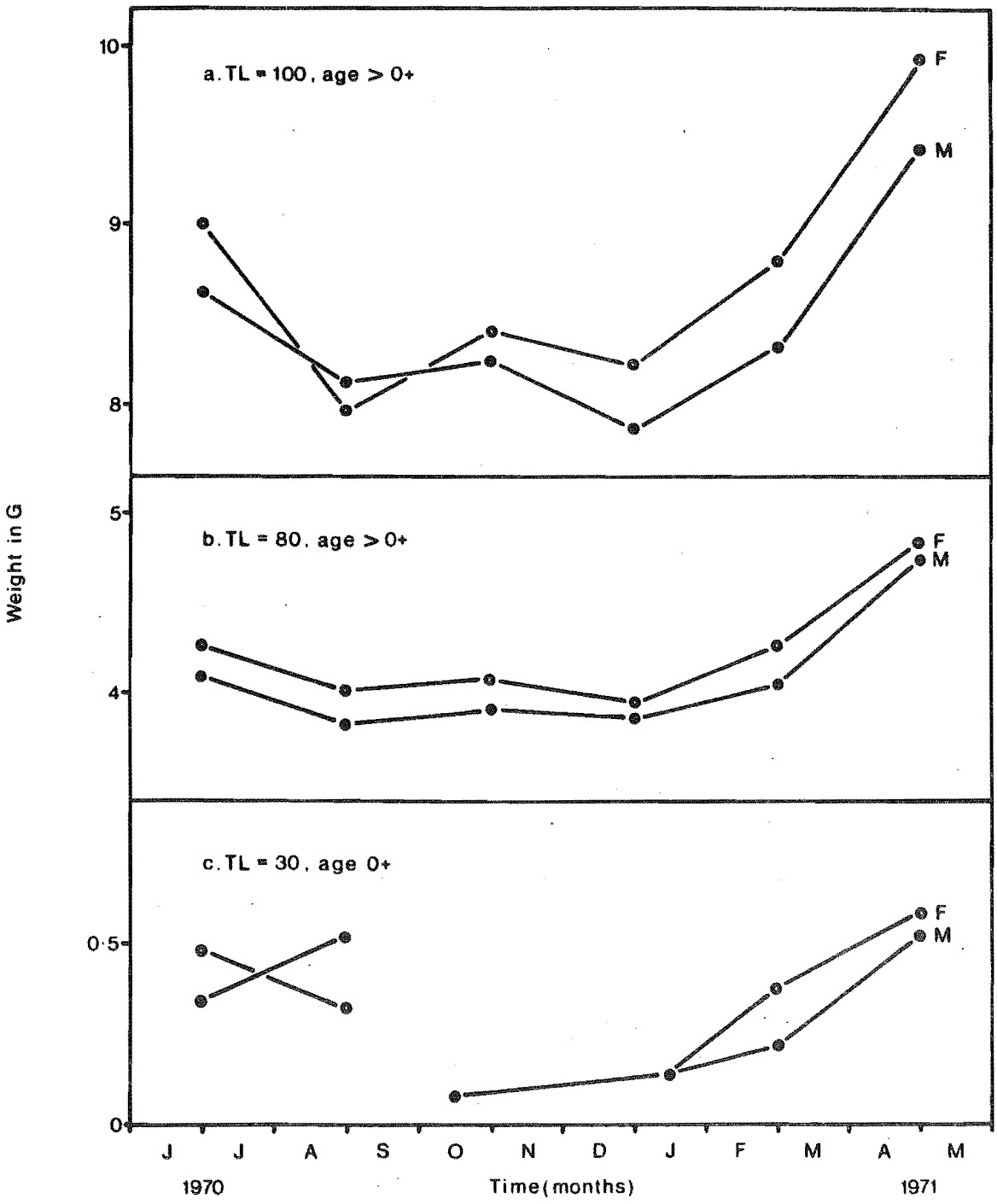
Values of b which differed significantly from 3.0 were detected using the formula (Snedecor and Cochran, 1967):

$$t = \frac{b - \beta}{S_b}$$

where t is a critical value of the t-distribution and has n-2 degrees of freedom, b is the observed gradient, β is the expected gradient (in this case $\beta = 3.0$) and S_b is the standard error of b.

In G. vulgaris immediately after hatching, in October and November, the b coefficient was not significantly different from 3.0. However, during the juvenile phase, from December to March, extremely high b coefficients were recorded for both males and females (see Table 7),

FIGURE 14. Bimonthly variation in the length:weight relationship of G. vulgaris. Points are predicted weight values calculated from bimonthly length:weight regressions (see Table 7) for males (m) and females (f) of three hypothetical TLs, viz. 100, 80 and 30 mm.

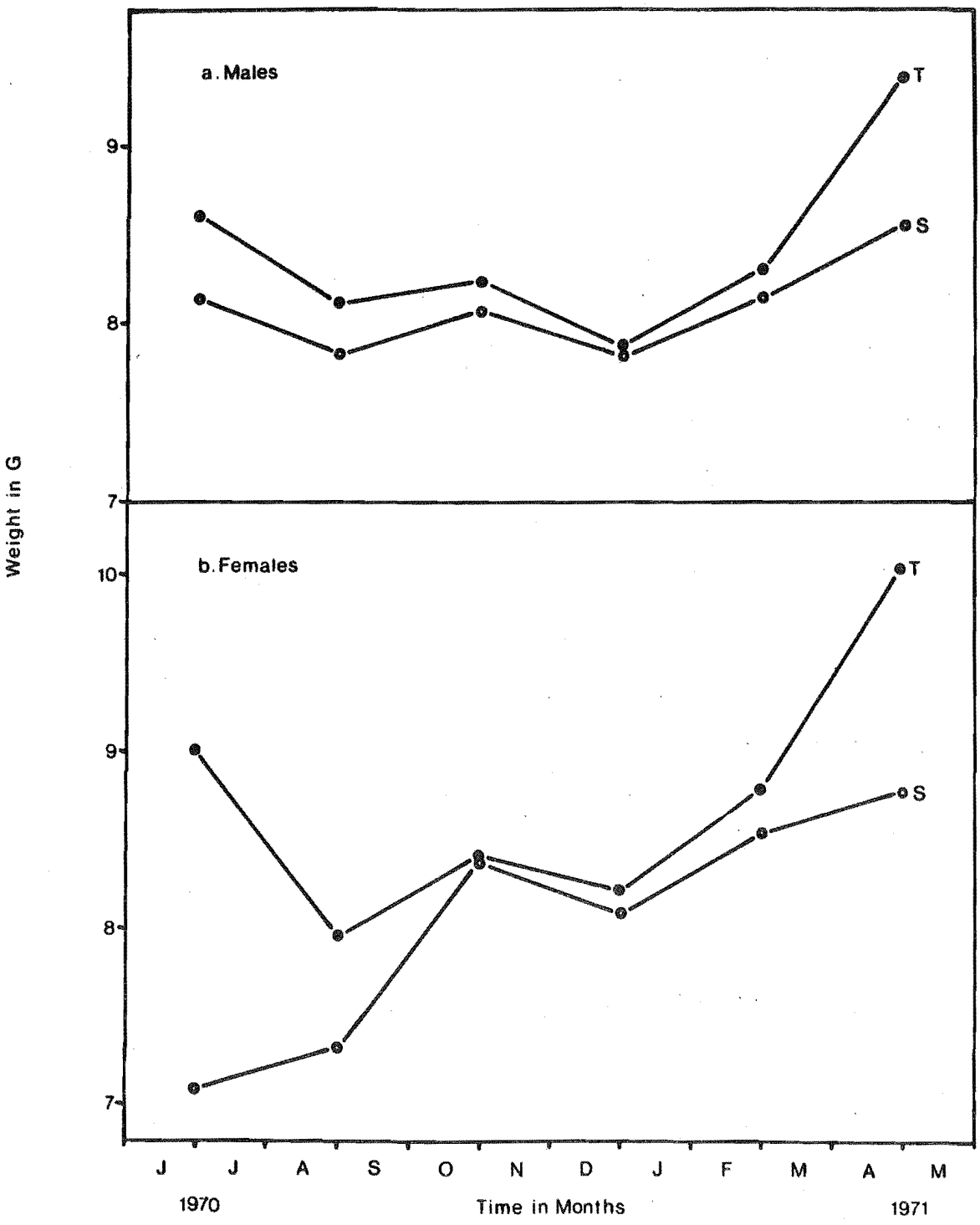

a. TL = 100, age > 0+
b. TL = 80, age > 0+
c. TL = 30, age 0+
F
M
10
9
8
5
4
0·5
0
Weight in G
J J A S O N D J F M A M
1970
Time (months)
1971

indicating a rapid increase in weight for a small increase in length. From the end of the juvenile phase to the end of the first year of life the b coefficients were again not significantly different from 3.0. Similarly, McPhee (loc. cit.), working with the largescale sucker, Catostomus macrocheirus, reported b coefficients of 4.9125 and 3.3496 for fish below and above 20 mm in length respectively. He concluded that the point of intersection of the two regression lines indicated the upper limit of the postlarval stage of development.

In female G. vulgaris older than age 0+ the b coefficient was significantly greater than 3.0 in eight out of twelve months; in males b tended to be lower than in females and was significantly greater than 3.0 in only four months. In both sexes b was significantly greater than 3.0 just before the breeding season and was reduced during spawning from August to September.

Unless the b coefficient is the same for all groups of fish whose condition is being compared, coefficient a cannot be used as a measure of their relative condition (le Cren, 1951). This applies particularly when changes in the two coefficients are correlated, which is usually the case (Hile, 1936). Thus, the regression line is affected by differential changes in weight in fish of different lengths. In G. vulgaris, coefficient b differed significantly between months for each group, and for both age groups of each sex, b was negatively correlated with a throughout the sampling period ($r = -0.972$ (males, age 0+); $r = -0.995$ (males, age >0+); $r = -0.974$ (females, age 0+); $r = -0.984$ (females, age >0+)). Therefore, for each group, changes in coefficient a could not be used to compare condition at various times of the year, and so changes in condition were considered in terms of predicted weight values for hypothetical fish of 30, 80 and 100 mm in length (using the regression coefficients given in Table 7) and are presented in Fig. 14. It can be seen that the condition of young-of-the-year fish increased throughout the growing season. In older fish, both males and females exhibited similar trends, with an increase in condition in late spring and autumn and a reduction in condition in early spring and summer. Females were generally in better condition than males except for a short period immediately after the breeding season.

FIGURE 15. Bimonthly variation in the length: weight (i.e. total weight) relationship (T) and the length: somatic weight relationship (S) for hypothetical male and female G. vulgaris of TL 100 mm.


a. Males
T
S
9
8
7
b. Females
T
S
10
9
8
7
Weight in G
J
J
A
S
O
N
D
J
F
M
A
M
1970
Time in Months
1971

To eliminate the effects of changes in gonad weight, regression lines were fitted to length:somatic weight (i.e. total weight of fish with gonad weight subtracted) data and modified condition factors were calculated. The modified condition factors followed the same trends as the condition factors based on total weights, indicating that somatic tissue undergoes seasonal changes, irrespective of gonad development. The bimonthly variation in the length:weight (i.e. total weight) relationship together with the bimonthly variation in the length:somatic weight relationship for a hypothetical fish of 100 mm in length is shown in Fig. 15. It can be seen that although both relationships follow the same trend in each sex, the development of gonads has a greater effect on condition in females than in males.

The above trends in condition were reflected in the fat deposits overlying the stomach and posterior part of the alimentary tract. Fat deposits were estimated in fish subsampled from regular monthly catches using a scheme based on that of Prozorovskaia (1951, cited by Nikolsky, 1963). Although chemical analysis, particularly the elucidation of the proportion of saturated and unsaturated fatty acids, is necessary for the most accurate results, visual estimation provides adequate information on seasonal trends in fat deposition in a number of fish species (Nikolsky, 1963). In G. vulgaris, fat deposits were at a minimum in spring after the breeding season; they increased in summer, reaching a peak in February and March, and were gradually reduced throughout autumn and winter.

Chapter IV

BREEDING BIOLOGY

1. Introduction

In a recent review, McDowall (1970) recognized two distinct life history patterns in the New Zealand Galaxiidae. Five species, G. maculatus, G. brevipinnis, G. fasciatus, G. postvectis and G. argenteus possess large numbers of small to moderate-sized eggs, they spawn generally in the autumn or early winter, and the newly-hatched larvae are carried to sea where they undergo further development. In the following spring, about six months later, the whitebait juveniles migrate back into fresh water in large, mixed-species shoals. Because of its commercial importance, the life history of G. maculatus has been extensively studied (see Woods, 1963, 1966; Burnet, 1965; Benzie, 1968a, b, c; McDowall, 1964, 1965b, 1968a). The diadromous habit has been eliminated in G. gracilis, a landlocked derivative of G. maculatus, which is thought to spawn in autumn (McDowall, 1970). Pollard (1971) investigated the life cycle of a landlocked form of G. maculatus in an Australian lake where he found that spawning occurred in streams flowing into the lake. Recently-hatched fish were washed downstream to the lake where they grew to maturity. The life cycles of G. brevipinnis, G. fasciatus, G. postvectis and G. argenteus are inferred mainly from the occurrence of their juveniles in samples of migrating whitebait. However, in some populations of G. fasciatus, and many of G. brevipinnis, the life cycle is restricted to fresh water (McDowall, 1970).

The other seven New Zealand galaxiids, viz. G. vulgaris, G. divergens, G. paucispondylus, G. prognathus, Neochanna burrowsius, N. apoda and N. diversus, are included in the second category of life history patterns. They have fewer and larger eggs, complete their life histories in fresh water, do not appear to migrate and have no whitebait stage (McDowall, 1970). Again, with few exceptions, e.g. G. vulgaris (Benzie, 1961 unpublished, 1968d) and G. divergens (Hopkins, 1971a), the life history patterns are poorly understood and few ecological investigations have been carried out to determine the sequence of events

associated with reproduction. The situation in N. burrowsius is unusual, because although it has large numbers of small eggs, its life history appears to be confined to fresh water (see Appendix 1).

Similarly, apart from G. maculatus, little information is available on the life histories of galaxiids in Australia (Frankenberg, 1966), South Africa (Jubb, 1965) and South America (Fischer, 1963; McDowall, 1971). In Australia, Galaxias coxii is thought to spawn in the normal adult stream habitat (Walford, 1928). In South America, Brachygalaxias bullocki appears to have an annual life cycle with large overwintering eggs, but occasional reports of large individuals suggest that some overwintering survival is likely (McDowall, 1971).

Benzie (1961 unpublished, 1968d) studied the life history of G. vulgaris with particular reference to embryological development. Data on sex ratios and the breeding season were also obtained. In the present study the reproductive biology of G. vulgaris was investigated in relation to fish of known age.

2. Maturity Cycles and Spawning Season

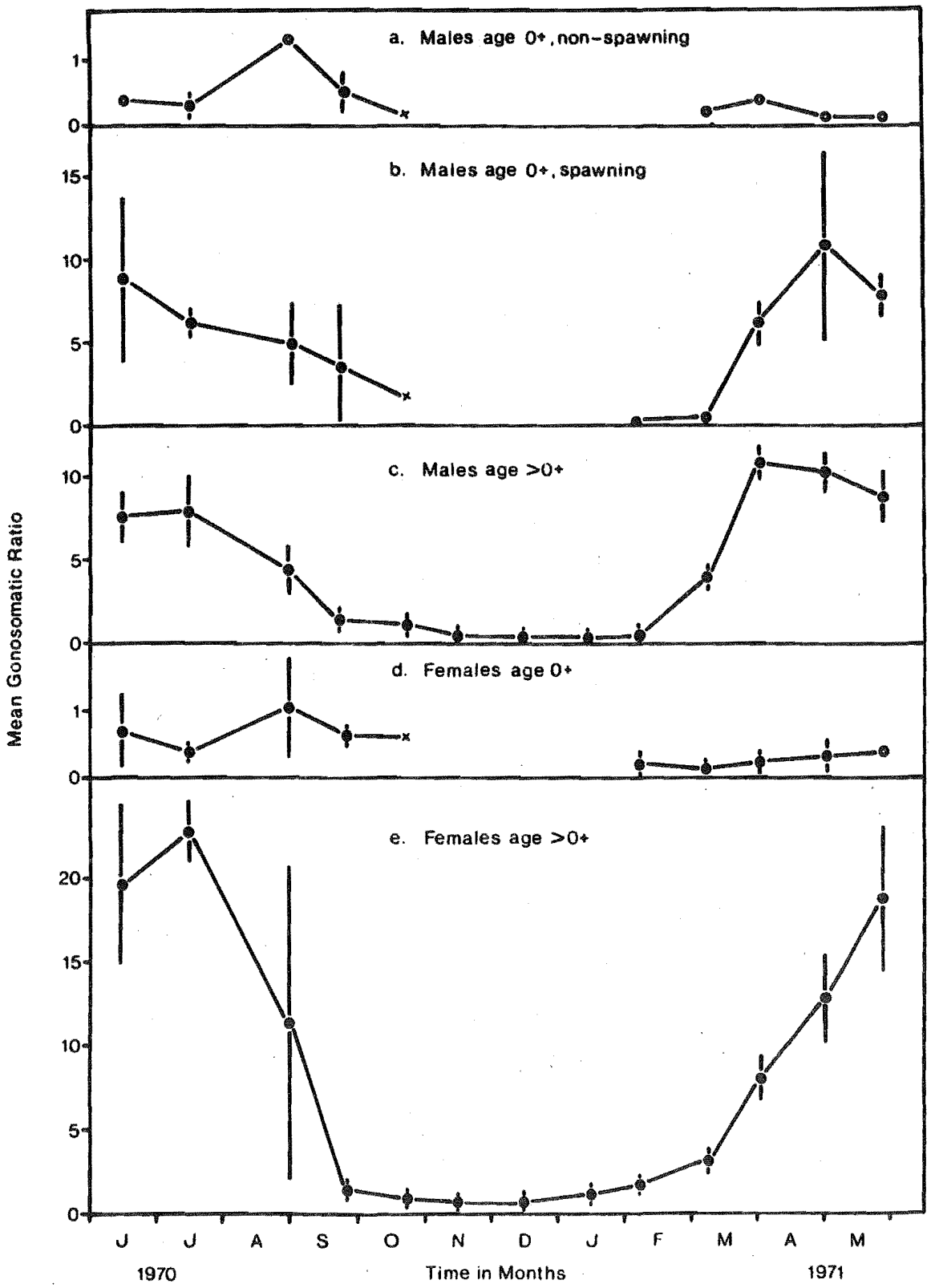
The spawning season of G. vulgaris was first defined by Stokell (1955) who stated that it occurred in winter and early spring. Benzie (1968d) found that G. vulgaris spawned in spring and early summer, while McDowall (1970) suggested that spawning occurred in early and middle spring. In the present study the spawning season was defined by following monthly changes in both the gonosomatic ratio and condition of the gonads in fish of known age. The gonosomatic ratio (GSR) was calculated from the formula:

$$GSR = \frac{\text{weight of gonads}}{\text{somatic weight}} \times 100$$

where somatic weight is the total weight minus the weight of the gonads. Thus, the weight of the gonads is expressed as a percentage of the somatic weight.

Females did not breed in their first year of life, so mean GSRs were calculated separately for females age 0+ and for females older than age 0+, all of which exhibited a similar reproductive cycle and were therefore treated as one group. Similarly for males, mean GSRs were calculated for the same two age groups. However, it was found that some

FIGURE 16. Monthly mean gonosomatic ratios of G. vulgaris from June 1970 to May 1971, (95% confidence intervals of the means are indicated by vertical bars). Note different Y-axis scales for females age 0+ and non-spawning males age 0+. (o indicates samples of less than five fish; x indicates age 1+ fish).


a. Males age 0+, non-spawning
b. Males age 0+, spawning
c. Males age >0+
d. Females age 0+
e. Females age >0+
Mean Gonosomatic Ratio
J J A S O N D J F M A M
1970
Time in Months
1971

males spawned in their first year of life, while others did not spawn until their second year. Accordingly, age 0+ males were further divided into those fish which spawned in their first year of life and those which did not spawn in their first year. Mean GSRs were not calculated until 3-4 months after hatching; all age 0+ fish sampled before this time were considered to be immature. The differences between the two groups of age 0+ males were not evident until March, 5-6 months after hatching. Mean GSRs, together with their 95% confidence intervals, for all groups, from June 1970 to May 1971, are presented in Fig. 16. It may be seen that spawning, indicated by the sharp reduction in GSR, occurred in late winter and early spring, between July and September. In age > 0+ females, the mean GSR began to increase in late summer; this trend continued throughout autumn and winter until just before the breeding season, when the ovaries reached nearly 23% of the somatic weight. In males, the mean GSR did not begin to increase until autumn; in both mature age 0+ fish and age > 0+ fish the testes reached nearly 11% of the somatic weight. The reduction in GSR in April and May for age > 0+ males, and in May for age 0+ males, is explained by an increase in somatic weight, rather than a reduction in gonad weight (see Fig. 15). In immature male fish aged 0+, and all age 0+ females, the gonad weight was generally less than 1% of the somatic weight for the whole of the sampling period.

The condition of the gonads throughout the reproductive cycle was recorded monthly using a scheme modified from those of Nikolsky (1963) and Laevastu (1965), in which the following stages were recognized:

I	Immature	Young individuals which have not yet engaged in reproduction; sexes cannot be distinguished externally; gonads small, inconspicuous and thread-like; eggs invisible to the naked eye; sex distinguishable only under high magnification (x100).
II	Ripening	Rapid increase in weight of gonads; sexes can be distinguished externally; eggs, dull yellow, visible to the naked eye; testes becoming creamy and less thread-like.

TABLE 8. Monthly maturity stages in G. vulgaris of known age (fish older than age 1+ are combined) from June 1970 to May 1971; I = immature, II = ripening, III = ripe, IV = spawning, V = spent, VI = resting; n = sample size. Note that age class changes between September and October samples, e.g. fish age 0+ become age 1+.

Maturity stage:			I			II			III			IV			V			VI		
Date	Sex	n	0+	1+	>1+	0+	1+	>1+	0+	1+	>1+	0+	1+	>1+	0+	1+	>1+	0+	1+	>1+
27,28-8-70	M	16	2	-	-	-	-	-	5	4	5	-	-	-	-	-	-	-	-	-
	F	13	5	-	-	-	1	1	-	3	3	-	-	-	-	-	-	-	-	-
25,26-7-70	M	65	10	-	-	-	-	-	21	28	6	-	-	-	-	-	-	-	-	-
	F	71	26	-	-	-	-	-	-	37	8	-	-	-	-	-	-	-	-	-
22-9-70	M	24	1	-	-	-	-	-	-	-	-	8	10	5	-	-	-	-	-	-
	F	21	8	-	-	-	-	-	-	-	-	-	4	1	-	2	6	-	-	-
19,20-9-70	M	19	6	-	-	-	-	-	-	-	-	6	3	4	-	-	-	-	-	-
	F	23	15	-	-	-	-	-	-	-	-	-	1	-	-	5	2	-	-	-
17-10-70	M	11	*	1	-	-	-	-	-	-	-	3	1	-	1	2	3	-	-	-
	F	12	*	3	-	-	-	-	-	-	-	-	-	-	-	4	5	-	-	-
14,15-11-70	M	21	*	1	-	-	-	-	-	-	-	-	-	1	-	9	10	-	-	-
	F	30	*	11	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	19
12,13-12-70	M	13	*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	7
	F	18	*	9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	9
16,17-1-71	M	9	*	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	4
	F	15	*	4	-	-	-	10	-	-	-	-	-	-	-	-	-	-	-	1
6,7-2-71	M	13	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	5
	F	16	5	-	-	-	2	9	-	-	-	-	-	-	-	-	-	-	-	-
6,7-3-71	M	11	2	-	-	2	2	5	-	-	-	-	-	-	-	-	-	-	-	-
	F	17	5	-	-	-	6	6	-	-	-	-	-	-	-	-	-	-	-	-
3,4-4-71	M	47	2	-	-	20	-	-	16	3	6	-	-	-	-	-	-	-	-	-
	F	64	54	-	-	-	3	7	-	-	-	-	-	-	-	-	-	-	-	-
1,2-5-71	M	15	1	-	-	-	-	-	6	2	6	-	-	-	-	-	-	-	-	-
	F	16	6	-	-	-	3	7	-	-	-	-	-	-	-	-	-	-	-	-
29,30-5-71	M	15	1	-	-	-	-	-	6	1	7	-	-	-	-	-	-	-	-	-
	F	11	2	1	-	-	3	5	-	-	-	-	-	-	-	-	-	-	-	-

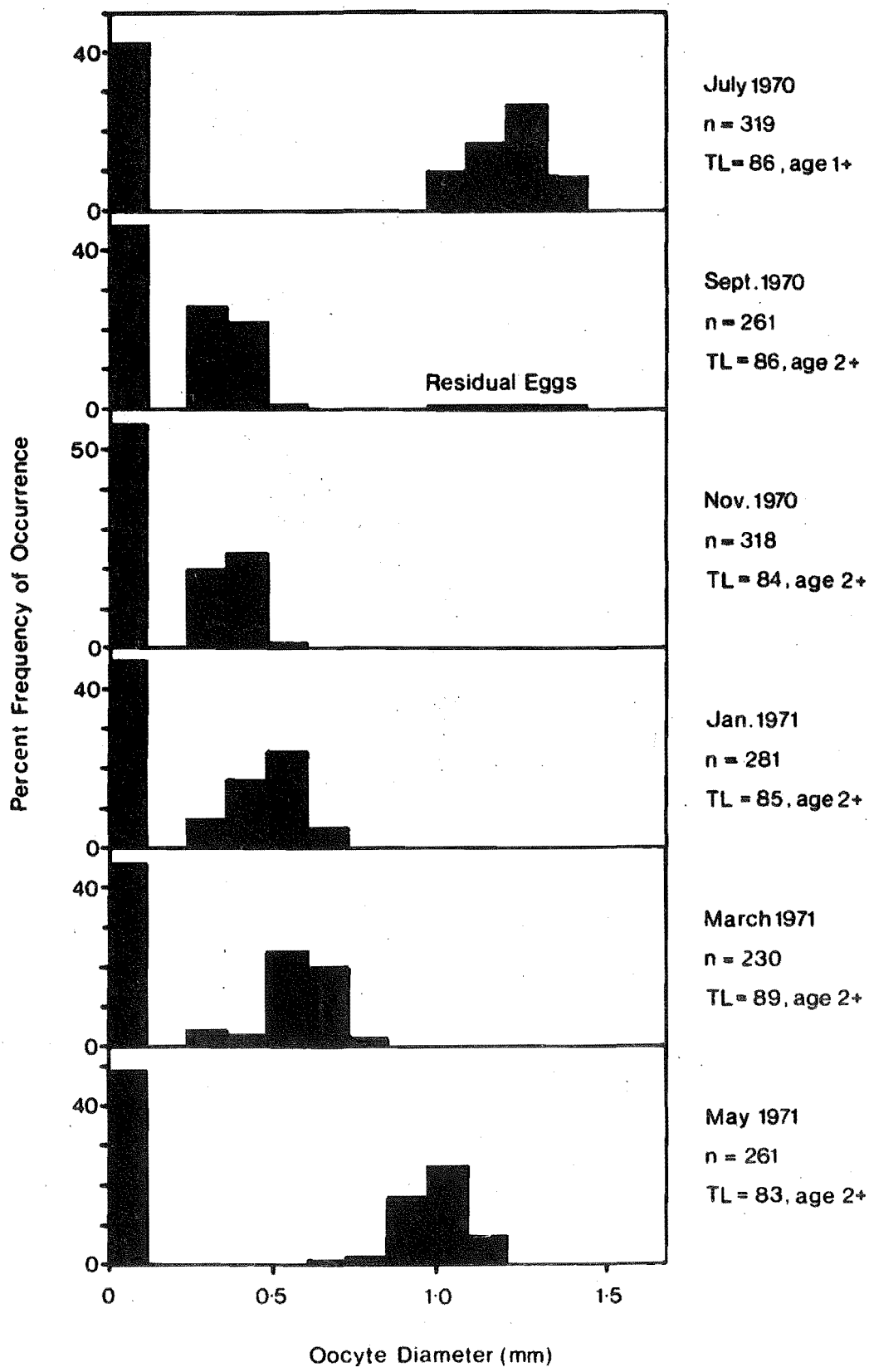
* indicates recently-hatched fish and juveniles; all immature

III	Ripe	Sexual products ripe; gonads have achieved maximum size, fill abdominal cavity; testes creamy white; sperm extruded under pressure; eggs large, yolky (bright yellow), readily seen with the naked eye, released only under heavy pressure.
IV	Spawning	Sexual products extruded in response to light pressure on the belly; weight of the gonads decreases rapidly from the start of spawning to its completion.
V	Spent	Sexual products discharged; gonads have appearance of deflated sacs; ovaries usually contain a few left-over eggs and the testes some residual sperm; testes appear quite dark because of surface melanophores lying closer together now that sperm has been discharged; sexes still distinguishable externally.
VI	Resting	Inflammation around genital aperture subsided; sexes cannot be distinguished externally; gonads smaller and less flaccid than in recently-spent fish; eggs not visible to the naked eye; testes thread or strap-like.

The maturity stages of fish aged 0+, 1+ and older than 1+ were recorded for each sex and are presented in Table 8.

The testes of some young-of-the-year males began to ripen in early autumn (March) only 5-6 months after hatching, at the same time as the testes of older males began to ripen. By the end of autumn it was possible to cause sperm to be extruded by applying pressure to the belly of a potential spawning male, so that at this stage males were considered to be ripe. This condition was maintained throughout winter until spawning occurred. Spent males were found in August and September. However, partially-spent males were recovered in October and November, which indicated that these fish had not completed spawning. The resting stage was slightly longer than in females (see next paragraph) and extended throughout the summer months, from December to February, until the testes began ripening again in early autumn. All males aged 1+ and older were found to spawn. Thus, the testes of those males which did not spawn in their first year began to ripen 17-18 months after hatching.

FIGURE 17. Percent frequency of occurrence of different-sized oocytes in ovaries of G. vulgaris sampled at two-monthly intervals from July 1970 to May 1971. (n = number of oocytes measured; TL = total length of fish in mm.).

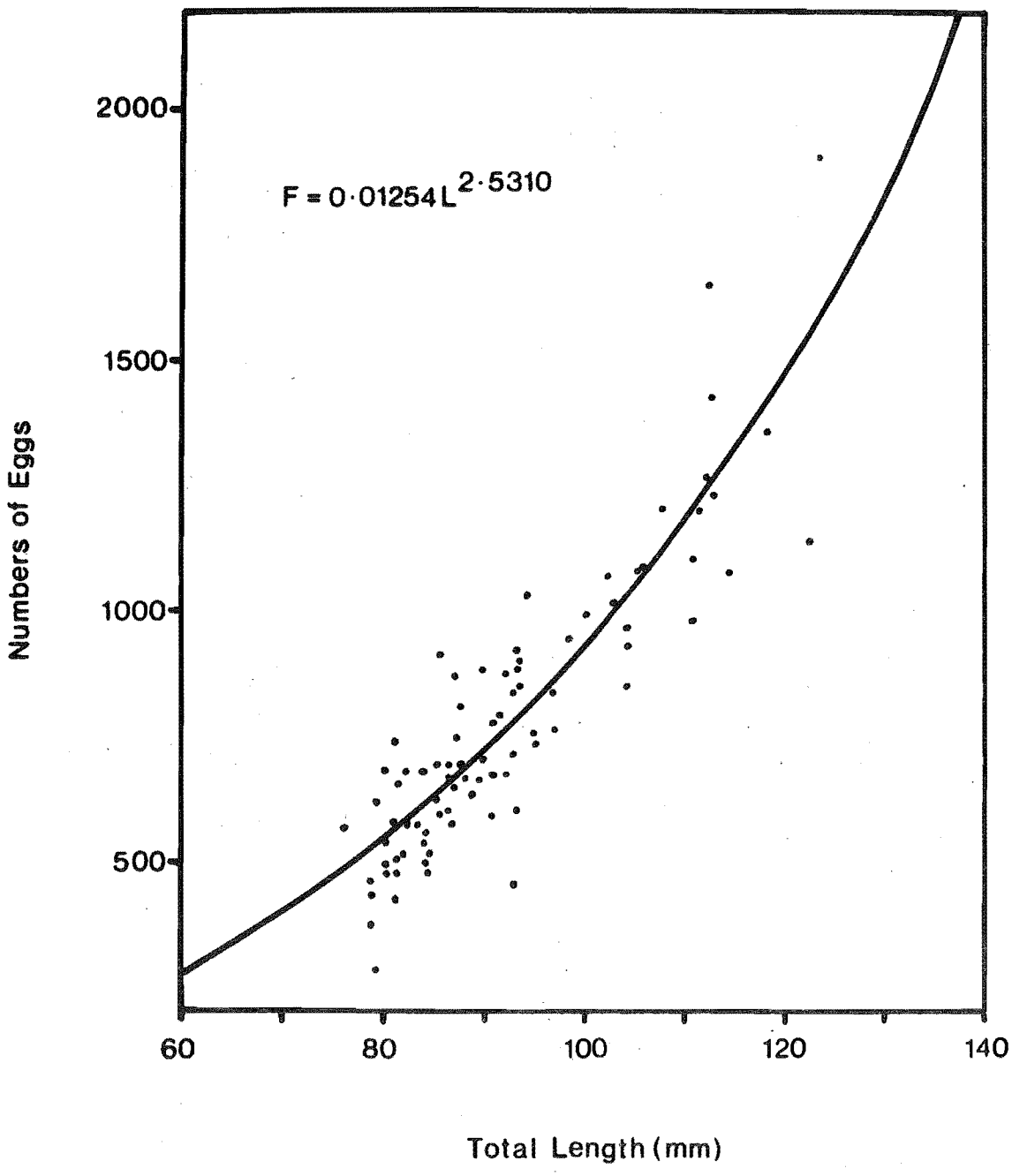

Percent Frequency of Occurrence
40
0
July 1970
n = 319
TL = 86, age 1+
40
0
Sept. 1970
n = 261
TL = 86, age 2+
Residual Eggs
50
0
Nov. 1970
n = 318
TL = 84, age 2+
40
0
Jan. 1971
n = 281
TL = 85, age 2+
40
0
March 1971
n = 230
TL = 89, age 2+
40
0
May 1971
n = 261
TL = 83, age 2+
0
0·5
1·0
1·5
Oocyte Diameter (mm)

As mentioned previously, no females spawned in their first year; ovaries first began to ripen in late summer of the second year of life, approximately 16 months after hatching. Ovaries of older fish also began to ripen in late summer and by the middle of winter all potential spawners were ripe. Spent females were found from August to October, and after a brief resting period in late spring and early summer (November and December) ovaries again began to ripen.

The maturation of eggs was investigated by examining the size frequency distribution and condition of oocytes in the ovaries of females taken throughout the regular sampling period. A number of workers (e.g. Clark, 1934: Mackay and Mann, 1969: Healey, 1971: Johnson, 1971) have used the analysis of size frequency distributions of oocytes at different times of the year in order to investigate the maturation cycle and frequency of spawning. In the ovaries of G. vulgaris, primary oocytes (see Cooper, 1952) are present on the ovarian wall and its infoldings, while recruitment eggs (i.e. oocytes in the process of maturation) and mature eggs are present in the central lumen. Because of this non-random intraovarian distribution, samples of oocytes were removed from a thin cross-section near the middle of the left ovary. The diameter of each oocyte was measured under a microscope using a micrometer eye piece. Since there was a great size difference between the primary oocytes and mature eggs, the magnifications used varied between x40 and x100. The percent frequency of occurrence of different sized oocytes in G. vulgaris taken at two-monthly intervals from July 1970 to May 1971 is presented in Fig. 17.

In July, just before spawning, the samples contained two distinct oocyte types, viz. small (<0.1 mm), translucent, primary oocytes and bright-yellow, mature eggs. In September, after spawning, all the mature eggs were shed, except for a few (usually less than 20) which would be resorbed; recruitment eggs, which give rise to next season's mature eggs, already were distinct from the primary oocytes. At this stage the recruitment eggs were translucent and slightly larger than the primary oocytes. Little change in this situation occurred until January when the rate of growth of the recruitment eggs increased. In March the presence of yolk gave the maturing eggs a pale yellow colour,

FIGURE 18. The relationship between fecundity (F) and total length (L) in G. vulgaris.


2000
1500
1000
500
F = 0·01254L^2·5310
Numbers of Eggs
60
80
100
120
140
Total Length (mm)

the intensity of which increased as more yolk was added. Growth and the deposition of yolk continued throughout autumn and winter until just before the breeding season.

An examination of the oocytes in virgin females revealed that recruitment eggs do not become distinguishable from primary oocytes until midsummer in the second year of life, not in early spring (September) as in the case of those fish which have already spawned.

The mean diameter of mature eggs in the July sample was 1.29 mm. This was corrected to 1.36 mm to take account of shrinkage produced by 10% formalin, in which the eggs were preserved. An appreciable increase in diameter occurs after the eggs have been shed; Benzie (1968d) reported a mean diameter of 2.6 mm in 200 naturally spawned G. vulgaris eggs.

3. Fecundity

Benzie (1968d) found a positive correlation between egg number and standard length in 25 mature G. vulgaris, in which the number of eggs ranged from 300 to 2,000. McDowall (1970) recorded 865 eggs in a female 83 mm long. In the present study, fecundity, i.e. the number of ripening eggs in a female prior to the next spawning period (Bagenal, 1966, 1968) was analysed in relation to total length, total weight and age, using data obtained from 84 fish taken from the River Glentui.

Both ovaries were removed from preserved (10% formalin) fish of known length, weight and age sampled just before the spawning season in 1970 and 1971. Ovaries were teased apart; the eggs were then hardened and freed from ovarian tissue by storage in Gilson's fluid (as modified by Simpson, 1951) for about three months (see Bagenal, 1968). Occasional shaking hastened the breakdown of the ovarian tissue. Total counts were made of the mature eggs in both ovaries, after they had been dried on filter paper.

Egg numbers varied between 284 and 1,911 per fish (see Fig.18).

Fecundity was related to length, weight and age by fitting regression lines (by the method of least squares - Sokal and Rohlf, 1969) to data transformed to logarithms. Such a transformation stabilizes

the variance with respect to fish size (Pope, Mills and Shearer, 1961; Bagenal, 1968) and has been used widely in fisheries investigations (e.g. Thomson, 1962; Hodder, 1963; Pitt, 1964, 1971; Hart, 1967; May, 1967; Wolfert, 1969; Mackay and Mann, 1969). The regression equations describing the fecundity (F) relationships of G. vulgaris were found to be:

for length (L)	$\log F = 2.5310 \log L - 2.0983$	
or	$F = 0.01254L^{2.5310}$	(see Fig. 18)
for weight (W)	$\log F = 0.7632 \log W + 2.2237$	
or	$F = 167.4W^{0.7632}$	
for age (A)	$\log F = 0.5944 \log A + 2.7831$	
or	$F = 606.8A^{0.5944}$	

Multiple regression techniques (Snedecor and Cochran, 1967) were used to analyse the relative effects of these parameters on fecundity. The results of these analyses are summarized in Table 9.

TABLE 9. Results of stepwise multiple regression analysis of fecundity against length, weight and age (all data transformed to logarithms).

Fecundity against	R^2 (coefficient of determination)	R (Multiple correlation coefficient-adjusted for degrees of freedom)
length	0.758	0.871
weight	0.814	0.902
age	0.544	0.738
length & weight	0.815	0.901
length & age	0.758	0.869
weight & age	0.823	0.906
length, weight & age	0.824	0.905

The coefficient of determination (R^2), i.e. the proportion of the sum of squares reduced by the variable(s), is highest for weight, of the single parameters. Weight and age together explain more of the variation in

fecundity, whilst the addition of length to these parameters does not increase greatly the amount of explained variation. Of the correlation coefficients (R), indicating the degree of association between fecundity and each of the variable(s), that for weight is the highest. The combination of weight and age further increases the association, producing a greater degree of association than the combination of all three parameters (when adjusted for degrees of freedom).

The relevance of the associations was then examined by calculating partial correlation coefficients for fecundity and each of the parameters in turn, using the formula (Snedecor and Cochran, loc. cit.):

$$r_{12.34} = \frac{r_{12.4} - r_{13.4}r_{23.4}}{\sqrt{(1 - r_{13.4}^2)(1 - r_{23.4}^2)}}$$

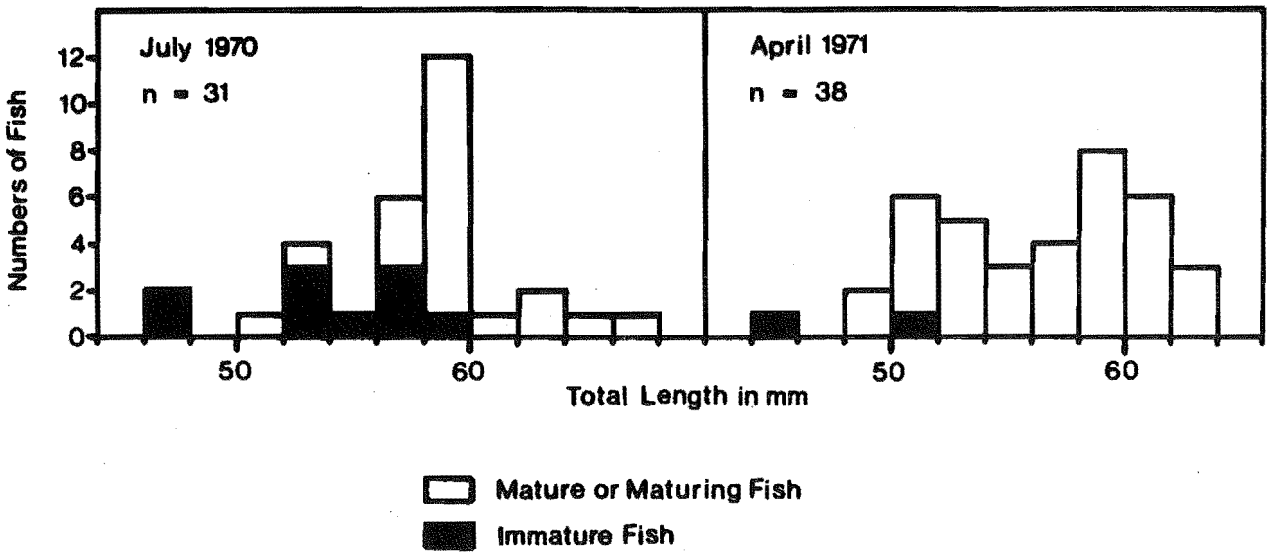
where $r_{12.34}$ is the correlation between variables 1 and 2, when variables 3 and 4 are held constant; similarly for $r_{12.4}$, $r_{13.4}$ and $r_{23.4}$. Thus, the correlation between fecundity and each of the variables in turn was calculated, while the other two variables were held constant. The results of this analysis are presented in Table 10, where it can be seen that the partial correlation coefficient for fecundity and age is significant and that for fecundity and weight is highly significant.

TABLE 10. Partial correlation coefficients for fecundity against length, weight and age (all data transformed to logarithms). (1 = fecundity; 2 = length; 3 = weight; 4 = age).

Fecundity against		Significance (d.f.=80)
length	$r_{12.34} = 0.0825$	$p > 0.05$
weight	$r_{13.24} = 0.5229$	$p < 0.01$
age	$r_{14.23} = 0.2184$	$p = 0.05 - 0.01$

These results indicate that weight is the most important factor influencing the fecundity of G. vulgaris. Since the partial correlation coefficient for

FIGURE 19. Relation between maturity and size of age 0+ males sampled in July 1970 and April 1971.


July 1970
n = 31
April 1971
n = 38
Numbers of Fish
0
2
4
6
8
10
12
50
60
50
60
Total Length in mm
Mature or Maturing Fish
Immature Fish

fecundity and length is not significant, the influence of length on fecundity may be attributed to the effects of weight and age at a particular length, rather than to the effect of length itself.

4. Relationship Between Maturity, Size and Age

The relationship between maturity, size and age has been reviewed and discussed by Alm (1959). He concluded that within an age class maturity is reached earlier by larger than by smaller fish, so that in each age class the growth rate and the attainment of a certain size decide the maturity. The age for maturity may be genetically determined or may depend on size, thus indirectly on growth rate. A number of environmental factors, especially temperature, probably affect the age at which maturity is attained.

The proportion of maturing and immature age 0+ males of G. vulgaris was determined by microscopic examination of the testes of fish in the April 1971 sample; out of 38 fish, 36 (95%) were maturing. The length frequency distribution of this sample (see Fig. 19) indicates that only fish which attain a certain size in early autumn become mature. Similarly, of the age 0+ males in the July 1970 sample (see Fig. 19), taken just before the breeding season, potential spawners (68% of all age 0+ males) were bigger than immature fish. This latter observation may be complicated by a change in growth rate once maturity was attained. A reduction in growth rate at maturity has been postulated by a number of workers (see Alm, 1959; p.125), although it has been discounted by Alm (loc. cit.) on the basis of extensive experimental observations. Such a change in growth rate would tend to decrease the growth rate of mature G. vulgaris in relation to immature fish of the same age, and thus reduce the difference between the two groups. However, there is little evidence for this in the July sample, in which immature fish are generally smaller than mature fish.

Up until 5-6 months after hatching all males were immature; in March the larger males began to mature, whilst the smaller males remained immature. This pattern was evident throughout the rest of the sampling period. The total length and condition (immature or mature) of age 0+ males, subsampled from regular monthly samples, are presented in Table 11. It may be seen that immature males are the smallest fish in each subsample.

TABLE 11. Total lengths (mm) of immature and mature (includes ripening, spawning and spent fish) age 0+ males sub-sampled from regular monthly catches in the River Glentui. (n = sample size) (mean = mean length (where available) of age 0+ fish, obtained from length frequency analysis of whole monthly samples).

Date	n	mean	Mature	Immature
27,28-6-70	7	57.8	61,61,59,59,54	51,47
22-8-70	10	-	70,69,66,65,65,64,60,58,53	53
19,20-9-70	9	58.3	63,60,55,52	56,56,55,52,48
17-10-70*	5	-	70,63,59,57	52
14,15-11-70*	9	61.4	64,62,61,61,59,59,58,57	54
6,7-3-71	4	51.4	53,52	47,43
1,2-5-71	6	61.6	68,65,60,55	54
29,30-5-71	7	63.5	68,64,60,59,58,56	54

* = age 1+ fish

Thus, it is evident that the attainment of maturity in male G. vulgaris depends on size. Fish which attain a certain minimum size in early autumn, as a consequence of a high growth rate, mature in their first growing season and take part in spawning 11-12 months after hatching. Fish with a lower growth rate fail to reach the critical size and remain immature until the following autumn. The length of the growing season may have an effect on the attainment of maturity. As pointed out in Chapter III, fish which hatch from early spawnings have a longer growing season than those which hatch from late spawnings and consequently stand a better chance of attaining maturity in their first year of life. However, no evidence was obtained to indicate that the fish which reached maturity were those which hatched early, or that the fish which remained immature were those which hatched late.

The proportion of age 0+, spawning males in each year probably depends on overall environmental conditions, so that in good conditions the growth rate is generally high and consequently more fish reach maturity, and vice versa in poor conditions. No evidence was obtained

to indicate any density dependent mechanism for determining the proportion of age 0+ males which mature.

In female G. vulgaris, ovaries did not begin to mature until the summer of the second year of life, approximately 16 months after hatching. Since the ovaries of all age 1+ fish generally matured at the same time, irrespective of size, (the size of age 1+ females in March 1971 ranged from 66 to 80 mm), it would appear that age is the most important factor affecting their maturity. That size may play some part in the attainment of maturity in females is indicated by one age 1+ female, 61 mm long, taken in May 1971. The ovaries of all other females aged 1+ had begun to ripen by late summer (February); this fish, however, still had immature ovaries containing small eggs invisible to the naked eye. It was much smaller than all other age 1+ females caught in May (mean length from length frequency analysis = 85.3 mm) so that its failure to mature may have resulted from its failure to reach a critical, minimum size. If this is the case it must be assumed that all of the other females examined had reached the critical size before maturation. This suggestion is feasible, the maturation of females depending on the attainment of a certain size, greater than that required by males, and usually reached in the second year of life. However, with the exception of this one female, the evidence suggests that age is the major factor affecting maturity of females. In either case, it is apparent that male G. vulgaris mature earlier, i.e. at a smaller size, than females. Thus, many males are mature in their first year of life, whereas no females mature until their second year of life. Benzie (1961, unpublished) noticed a similar situation in the G. vulgaris population inhabiting the Cass River.

5. Sex Ratio

Benzie (1968d) reported ratios of male:female G. vulgaris ranging from 14:1 to 1:2 in samples taken from five Canterbury rivers. However, it is unlikely that representative samples of the populations were obtained, since the samples were collected by hand, a subjective sampling method (Benzie, pers. comm.). Electric fishing is one of the least selective of fishing methods (see Chapter I) and its use in the present study enabled more representative samples of the River Glentui population to be obtained. The sex ratio in each of five samples in which

the sex of all fish was determined is presented in Table 12. In all cases the ratio does not differ significantly from 1:1. This ratio applies to all individuals irrespective of whether they are spawning or non-spawning fish.

TABLE 12. Sex ratios of G. vulgaris.

Sample	Males	Females	χ^2(d.f.=1)	Signif.
27,28-6-70	45	43	0.0455	$p > 0.5$
25,26-7-70	65	71	0.2647	$p > 0.5$
19,20-9-70 (>0+)	21	29	0.6400	$p > 0.1$
3,4-4-71	121	126	0.1052	$p > 0.5$
1,2-5-71	83	97	0.5444	$p > 0.1$
Total	335	366	0.6854	$p > 0.1$

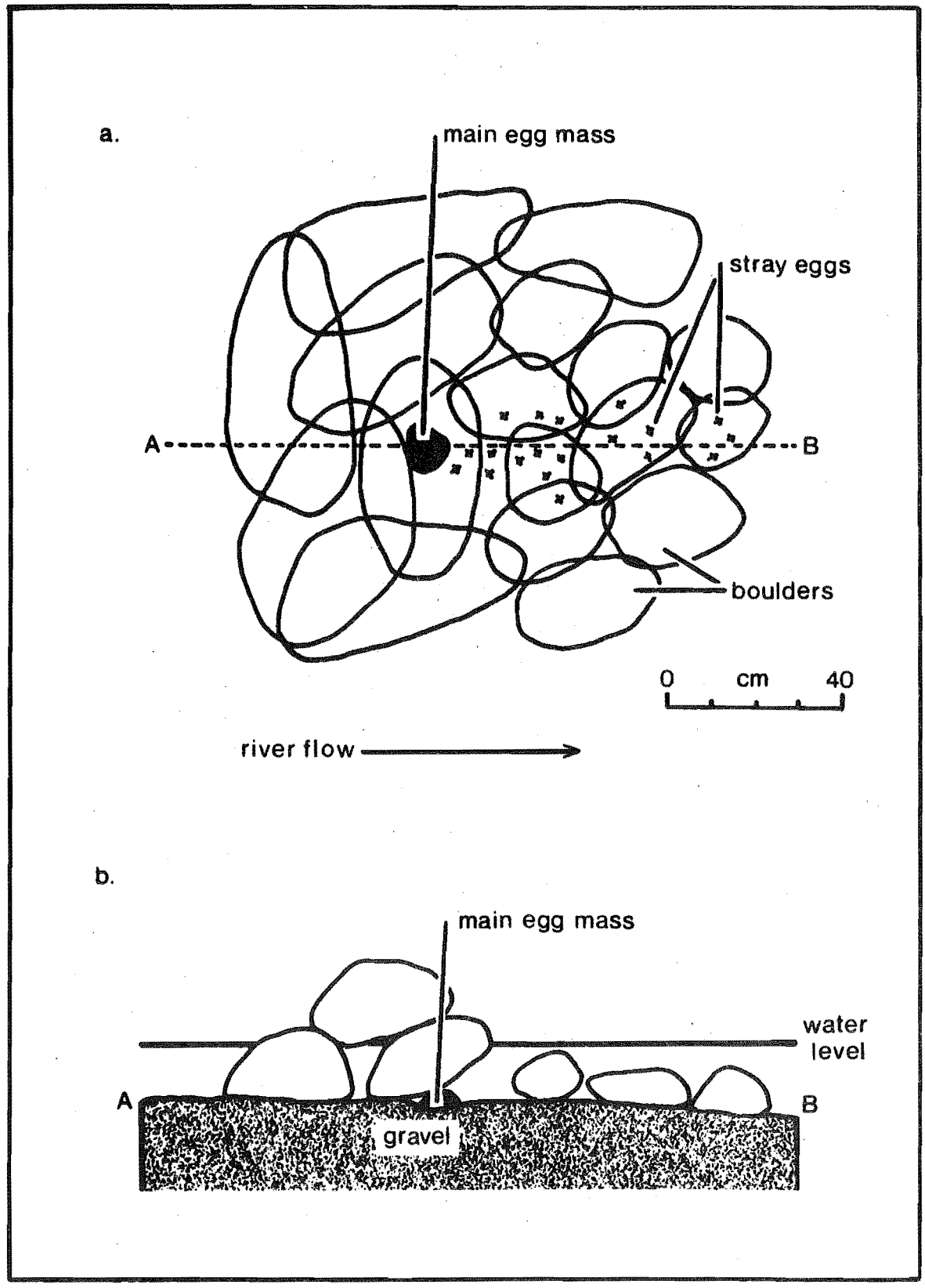
The sex ratio of potential-spawning fish was determined in the July 1970 and April 1971 samples, details of which are presented in Table 13.

TABLE 13. Sex ratios of potential-spawning (p.sp.) G. vulgaris, (imm. = immature).

Sample	Age	Males		Females		χ^2(d.f.=1)	Signif.
		p.sp.	imm.	p.sp.	imm.		
25,26-7-70	>0+	34	0	45	0		
	0+	21	10	0	26		
	0+,>0+	55	-	45	-	1.000	$p > 0.1$
3,4-4-71	>0+	83	0	72	0		
	0+	36	2	0	54		
	0+,>0+	119	-	72	-	11.568	$p < 0.005$

In July 1970, although there were more potential-spawning males than potential-spawning females, the sex ratio was not significantly different

FIGURE 20. A typical nest site of G. vulgaris.


a.
main egg mass
stray eggs
A
B
boulders
0
cm
40
river flow
b.
main egg mass
water
level
A
B
gravel

from 1:1. However, in April 1971, the ratio was significantly different from 1:1, there being more males than females. The larger number of potential-spawning males was due mainly to the presence of age 0+ fish; all age 0+ females were immature and so did not contribute to the spawning population.

Thus, in the River Glentui during the sampling period, the total sex ratio was 1:1. However, the sex ratio of potential-spawning fish indicated that more males than females took part in the spawning process. The preponderance of spawning males is correlated with the different behavioural roles of the two sexes at spawning, and is discussed later.

6. Spawning

Information on spawning of G. vulgaris was obtained from extensive sampling in the River Glentui during the spawning seasons of 1970 and 1971, particularly 1971, together with laboratory observations in a stream tank (for description, see Chapter VII) and standard aquaria.

Spawning in the River Glentui usually occurred in the most turbulent parts of a riffle area, the normal adult habitat. However, just before spawning, there was a small, but distinct, upstream movement of all G. vulgaris (see Chapter V), so that for any one fish, spawning probably occurred upstream from the area which it normally occupied throughout the rest of the year and to which it returned after spawning was completed. The overall significance of these movements is discussed in Chapter V.

(1) The nest site and characteristics of the egg mass

Nests (i.e. places where eggs are deposited) were made on a gravel substrate beneath a large boulder, a common situation for many stream-dwelling fish (see Allen, 1969a; Hynes, 1970a). A saucer-like depression was made in the gravel; the diameter of the rim of the depression varied, but was usually between 10 and 12 cm, whilst the depth of the excavation at the centre was 2-3 cm. The flow of water over the nest was reduced by the situation of the depression immediately downstream from boulders. A diagram indicating the position of the nest, based on the examination of 15 nests found in the River Glentui, is presented in Fig. 20. The eggs were laid in the centre of the depression, where most remained on the surface of the gravel, with a few eggs being

TABLE 14. Number of eggs in G. vulgaris nests found in the River Glentui, together with the number (N) and condition of fish found within 1 m of the nest. (P.sp. = partly spent; sp. = spent; imm. = immature).

Nest	Date	No. of eggs	Males			Females			
			N	Ripe	P.sp.-sp.	N	Ripe	Sp.	Imm.
1	21-8-71	2,714	7	1	6	2	1	1	0
2	26-8-71	702	0	-	-	0	-	-	-
3	27-8-71	862	1	0	1	0	-	-	-
4	27-8-71	722	0	-	-	1	0	0	1
5	4-9-71	983	1	0	1	0	-	-	-
6	4-9-71	468	2	1	1	0	-	-	-
7	4-9-71	881)							
		)	2	1	1	3	2	1	0
8	4-9-71	1,158)							
9	10-9-71	715)							
		)	12	7	5	2	0	0	2
10	10-9-71	874)							
11	14-9-71	2,566	1	0	1	0	-	-	-
12	14-9-71	809)							
		)	2	1	1	0	-	-	-
13	14-9-71	710)							
14	14-9-71	648	0	-	-	1	0	1	0
15	16-10-71	336*	4	0	4	0	-	-	-

* eggs in this batch had already begun to hatch.

found amongst the loose gravel underneath. The egg mass was roughly circular, with a diameter of 4-6 cm, and was usually 4-8 eggs thick. The eggs were stuck to each other and the lowest layer adhered to the substrate. In one instance an egg mass was found wedged between the substrate and a boulder so that approximately equal numbers of eggs were attached to both substrate and boulder. Normally, the only eggs found on the underside of boulders were those swept downstream from the nest. The occurrence of such stray eggs has been reported for other species, particularly salmonids, which lay their eggs in similar situations (Greeley, 1932; Hobbs, 1937). Eggs scattered downstream are less likely to survive than those in the egg mass; they are more likely to be eaten by predators or swept to other situations unsuitable for their further development. The number of eggs which stray downstream depends on a number of factors, such as the height of the female's vent above the gravel at the time of laying, and the water current above the nest. For one isolated egg mass, the number of stray eggs was estimated by closely examining the gravel and boulders up to 2 m downstream from the nest. The eggs found in this way amounted to 3% of the number of eggs in the nest, but this figure did not include any eggs which might have been washed completely out of the area, so that the figure of 3% must be regarded as a conservative estimate.

The number of eggs in each nest found in the River Glentui is presented in Table 14. Since the maximum number of eggs recorded in G. vulgaris taken from the River Glentui was 1,911 (see section 3 of this Chapter), and the mean for all females examined was 777, it may be seen that at least two nests contained more eggs than could have been laid by one female. In one instance, all the eggs appeared to be at the same stage of development, while in the other, eggs at two different stages of development were recognized. Nests were generally found singly, but on three occasions (Table 14: nests 7-8, 9-10, 12-13) two nests were found less than 30 cm apart, under the same boulder.

The positioning of the nest site within the riffle area is important. As mentioned previously, spawning occurred in the most turbulent parts of the riffle; this was usually at its upstream edge. The egg mass was sheltered to some extent from the effects of the current,

but some movement of water is necessary all around the eggs, including water movement through the gravel on which the eggs are laid, in order to carry oxygen to the developing eggs. This is enhanced by the presence of loose gravel within the nest and also by making the nest in a position where movement of water through the gravel occurs, such as at the downstream edge of a pool where the water flows into a riffle area (Stuart, 1953a, b, 1954). Thus, any nests made at the upstream end of a riffle will have water flowing through the gravel in which the eggs are laid. The oxygen content of the interstitial water is greatly affected by movement of the water and has been shown, by Wickett (1954) and McNeil (1962), to be correlated with the hatching success of pink (Oncorhynchus gorbuscha) and chum (O. keta) salmon. Thus, the choice of a spawning site by G. vulgaris depends on finding a situation where there is an adequate flow of water through the gravel. Since the eggs are not usually buried in the gravel, but merely lie in a depression in the gravel, the protection of boulders is necessary in order to prevent the egg mass from being dislodged by the strong flow of water above the gravel which occurs at the head of a riffle.

Although the egg mass may be up to eight eggs thick, its honeycomb nature, with spaces between the spherical eggs, permits water to percolate through the mass and so carry oxygen to the innermost eggs.

From laboratory observations it appears that a gravel substrate is essential for spawning to occur. Ripe fish kept in glass or perspex aquaria failed to spawn, although cover was provided in the form of boulders. Further, it appears that gravel of a certain minimum depth is required. On four occasions nests begun in shallow gravel were abandoned, apparently because the floor of the aquarium prevented the making of a sufficiently deep depression. However, these factors are unlikely to be limiting in the natural situation.

(2) Behaviour during the spawning period

For most of the year, G. vulgaris leads a solitary life and is generally nocturnal. However, in August and September there is a reversal of the normal diel activity pattern, so that both males and females become essentially day-active (see Chapter VI, Fig. 36).

Associated with this reversal, there is an increase in aggressive behaviour; this is not merely the result of an increase in the number of encounters. Whilst sampling in the River Glentui, all fish were kept in perspex aquaria (40 x 30 x 20 cm) containing 20-30 fish each; no substrate or cover was provided. Only in August and September were aggressive encounters observed, even though fish were kept in similar conditions throughout the year. The aggressive behaviour observed in these aquaria, and also in laboratory aquaria, consisted of approaching, chasing and biting. No elaborate displays were observed. Approaching consisted of a fish, usually with its mouth open, swimming directly towards another fish. Such approaches were made by fish regarded by the observer as being at their own station (see section 1.(2) (b) of Chapter VII) and normally started when the resident fish was resting on the substrate. Approaching normally resulted in swimming away by the fish approached, in which case chasing occurred for a short distance (not more than 20 cm in laboratory aquaria). Once the intruder had fled, the resident fish returned to its station. However, on a few occasions, particularly in the perspex holding aquaria which offered no cover for the fish, biting occurred. Bites were inflicted mainly on the caudal fin, although other parts of the body were also bitten. The encounters described above were generally intraspecific, although on one occasion a G. vulgaris female, of total length 77 mm, was seen to bite a large P. breviceps male (TL 70 mm). Although no quantitative estimates were made, it appeared that males were more aggressive than females, and that this aggression was directed at females rather than at other males. The significance of this aggressive behaviour is discussed later.

In all spawnings and attempted spawnings in laboratory aquaria, the male appeared to choose the nest site and subsequently prepared it for spawning. The female took little part in the preparation of the site until it was almost completed. The depression in the gravel was made by vigorous undulations of the body which caused gravel to be swept out of the depression and carried away by the water current. The activity resembles the "cutting" of pits by Salmo salar, as described by Jones (1959), which occurs in most species of salmon and trout which inhabit running waters (see Hynes, 1970a). However, with G. vulgaris, the

whole affair is on a much smaller scale than in the case of S. salar. Further observations are required before a detailed description of the nest-making process in G. vulgaris can be presented.

Although the actual spawning process was not observed, two significant facts concerning it were established from observations made on pairs of fish which spawned in laboratory aquaria. After each spawning, it was found that females had shed all their eggs, whereas males had not shed all their sperm. These observations were confirmed by the examination of fish taken from the River Glentui during the spawning period. The ovaries of females were either fully distended or completely emptied of ripe eggs. No intermediate condition was found although on a few occasions a small number of residual eggs were present. On the other hand, the testes of males sampled during the spawning season were found to contain varying amounts of sperm. Since, immediately before the spawning season, the testes of all mature males were completely filled with sperm, it is evident that males shed sperm on more than one occasion in each spawning season. This is confirmed also by an examination of the GSR of individual fish sampled during the spawning period. The GSRs of females were either very high (before spawning) or very low (after spawning), whereas the GSRs of males were often intermediate between the values obtained during the pre- and post-spawning periods.

Most of the observations made in the laboratory during the spawning season were based on pairs of fish. However, some pertinent observations were made on one group of six males; this group consisted of two fish aged 0+, the rest being older than age 0+. Observations were made at regular intervals (at least three hours apart) between 15-7-71 and 2-8-71. The older fish spent most of their time in a depression which they had made in the gravel beneath a large boulder; all four were frequently seen together, often in bodily contact. The depression was identical to that used for spawning purposes; at other times of the year, although living under and between boulders, G. vulgaris was not seen to make depressions in the gravel. The age 0+ fish in the group were observed with the older fish only on a few occasions (3% and

7% of 45 observations in each case) and did not appear to show a preference for any one particular site.

(3) Attachment to the nest site

The degree of attachment of males and females to the nest site was indicated by both field and laboratory observations. In the River Glentui during the 1971 spawning period, the number and condition (ripe, spent, immature) of fish caught within a radius of one metre of each nest was recorded; these data are presented in Table 14. More males (32) than females (9) were caught near the nests and, of the females, three were immature; no immature males were found near the nests. All the immature females and four of the 32 spawning males were aged 0+; all other fish were older than age 0+. The ratio of 32:9 at the nest site is significantly different ($p < 0.005$) from a 1:1 ratio ($\chi^2 = 12.90$, d.f. = 1). Also, the observed ratio of sexually mature fish is significantly different ($p < 0.01$) from the ratio of 1.65 males: 1 female ($\chi^2 = 7.756$, d.f. = 1) expected on the basis of the number of potential-spawning fish in the April 1971 sample (see Table 13). In each case there is a significant excess of males, indicating that males are more attached to the nest site than are females. Spent females were found in greater numbers in the more quiet parts of the riffle, away from the nest sites. That males are attached to the nest site after spawning is indicated further by observations made by Benzie (1961 unpublished; 1968d), who found only males or occasional unspawned females in association with egg masses of G. vulgaris in the Cass River.

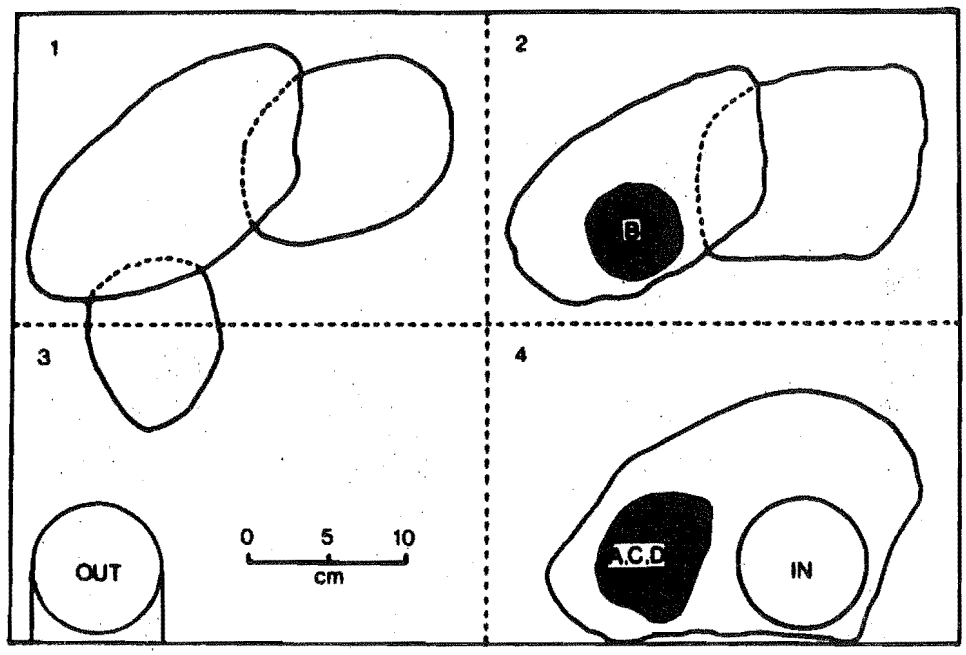
The attachment of the male to the nest site was indicated also by observations made in four running-water aquaria (61 x 38 x 38 cm) each with a substrate of gravel (5 cm deep) and boulders. The boulders were arranged in similar positions in all four aquaria and the depth of water in the aquaria varied between 6 and 8 cm. In August and September 1971, two series of spawnings were attempted. In each series, one ripe male and one ripe female were placed in each aquarium. Out of eight pairs, four were successful. Each successful pair produced a single egg mass which was laid in a depression in the gravel beneath a boulder. The standard topography of the bottom of each aquarium in which spawning occurred, together with the locations of the egg masses, is shown in

FIGURE 21. a. Standard topography of the bottom of four aquaria, with substrate of gravel and boulders, used in G. vulgaris spawning trials (see text). Egg masses, each laid in a depression in the gravel under a boulder, are indicated by heavy shading. In trials A, C and D, the egg mass was laid at the same site in section 4; in trial B, the egg mass was laid in section 2.

b. Percent frequency of occurrence of fish in each section of the aquarium after egg laying (see text). The table below gives details of the four pairs of successful fish, including the total length (TL) of each fish in mm, and the number of observations (N) in each trial.

		Males		Females			
egg mass	section	TL	age	TL	age	N	date
A	4	101	3+	98	2+	50	26-8-71 - 13-9-71
B	2	88	2+	96	2+	58	6-9-71 - 8-10-71
C	4	71	1+	95	2+	39	27-8-71 - 13-9-71
D	4	83	2+	96	2+	57	22-9-71 - 21-10-71

a


1
2
B
3
4
OUT
0 5 10
cm
A,C,D
IN

b

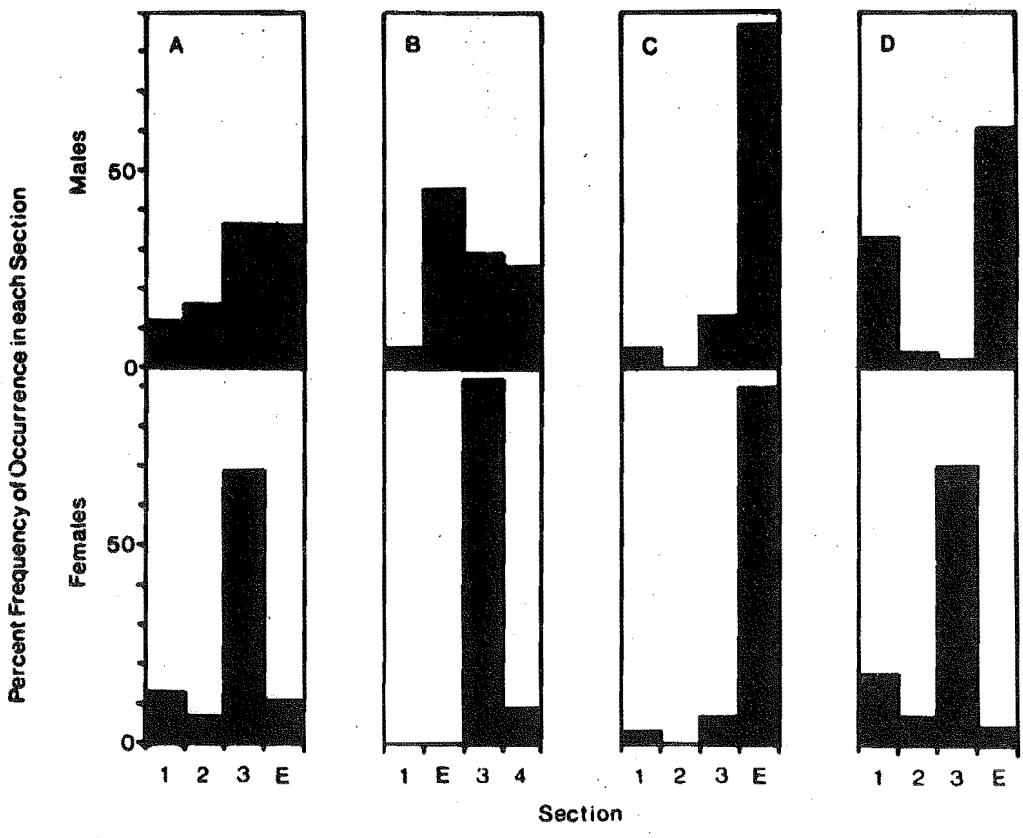

Percent Frequency of Occurrence in each Section
Males
Females
50
0
50
0
A
B
C
D
1 2 3 E
1 E 3 4
1 2 3 E
1 2 3 E
Section

Fig. 21a. Each aquarium was divided into four sections and the position of each member of a pair was recorded at intervals (at least three hours apart), starting from when the egg mass was discovered, which was usually not more than six hours after the eggs were laid. For each section, the percent frequency of occurrence of each fish in a successful pair, is presented in Fig. 21b. It may be seen that females, with one exception, tended to spend more time in section 3, where they positioned themselves between the outflow pipe and the side of the aquarium. In trial C, the female, although spending most time in the section containing the egg mass, usually was found resting on top of the large boulder immediately below the inflow pipe, and not beneath the boulder with the egg mass. On the other hand, males were found to spend more time in the section containing the egg mass than in any of the other sections. When found in the section containing the egg mass, the male was invariably beneath the boulder under which the eggs were laid. No fanning movements were observed. No eggs were found in the stomachs of any of the fish at the end of each experiment. Since each egg mass eventually succumbed to an infection of Saprolegnia sp., no observations were made on the relationship between newly-hatched fish and their parents. The lower eggs in each mass probably died because of an inadequate supply of oxygen caused by the low rate of water flow, particularly in the substrate, in the experimental aquaria. Once these eggs became infected, the fungus quickly spread to the rest of the egg mass.

(4) Environmental factors affecting spawning

Vlaming (1972) critically reviewed the literature concerning the environmental control of teleost reproductive cycles. He pointed out that although photoperiod was generally regarded as the dominant regulatory factor in temperate regions, photoperiodism appeared to be temperature sensitive in the majority of teleosts studied.

The maturation of gonads in G. vulgaris began in late summer and autumn, at a time of decreasing photoperiod and decreasing temperature. A similar situation was found in G. maculatus by McDowall (1968a) and Pollard (1971), and also in Neochanna burrowsius (see Appendix 1). In G. maculatus the spawning migrations were found to be cyclic and were correlated with lunar and tidal effects (Burnet, 1965; Benzie, 1968a;

McDowall, 1969a, 1970). In G. vulgaris spawning occurred in late winter and early spring when both photoperiod and water temperature were increasing. No experimental studies were undertaken in order to determine the relative importance of environmental factors in controlling the reproductive cycle, but observations made in the River Glentui indicate that temperature may affect the onset of spawning.

The proportion of spent fish in samples of mature, female G. vulgaris taken in three sections of the River Glentui during the spawning season of 1971 is presented in Table 15.

TABLE 15. Proportion (%) of spent females in samples of mature G. vulgaris taken in three sections of the River Glentui during the spawning season of 1971 (see text) (N = number of mature females in each sample) (the figures in parenthesis are the approximate distances in km from the middle of Section A).

Date	N	A(0)	B(1.5)	C(4.5)
16,17,18-8-71	61	-	-	38
21,22-8-71	39	-	28	-
26,27-8-71	26	-	-	61
2-9-71	15	-	47	-
5-9-71	7	0	-	-
10,14-9-71	30	-	87	-
21,22,26-9-71	68	-	-	100
16-10-71	16	-	100	-

Working upstream, the first section was that of the home range investigation (C), then the regular sampling section (B) and finally a small section of riffle (A) within the system of waterfalls (see Fig. 1). Although in some cases the sample sizes are small, it is evident that spawning started earlier in section C than in section B, and that spawning in these two sections started earlier than spawning in section A. On 5-9-71 spawning had not started in section A, although in the other two sections the spawning season was well advanced. Thus, spawning

began earlier in the lower reaches than in the more upstream sections. Similarly, Benzie (1968d) noticed that spawning in the Cass River started earlier towards the mouth of the River than it did towards the source and that the onset of spawning was affected by water temperature. In the River Glentui, photoperiod was considered to affect all three sections to the same extent, although the light intensity in section A was relatively low compared with sections B and C because of the gorge-like nature of the area. Air temperatures varied between the sections, but exhibited no trend. However, there was a marked gradient in water temperature, with the lowest temperature being recorded in the upstream section (A) and the highest temperature being recorded in the downstream section (C) (see Table 16).

TABLE 16. Air and water temperatures (^{o}C) in three sections (A, B, C) of the River Glentui (see text).

		A	B	C
Water (7, 10-9-71)	Max.	6.7	8.3	12.5
	Min.	2.2	3.9	4.2
Air (10, 12-9-71)	Max.	20.6	18.6	19.4
	Min.	4.7	5.9	5.6

Thus, there is a correlation between temperature and spawning, with spawning starting earlier in the warmer parts of the River. Since spawning takes place after an upstream movement, it is possible that this movement may also be affected by temperature.

Spawning occurred at a time when rainfall in the area is typically low (see Fig. 3c) and, consequently, when the rate of water flow in the River Glentui is reduced. At times of reduced discharge the number of potential-spawning sites in turbulent riffles become reduced, so that the reduced rate of flow may have the effect of concentrating potential spawning fish in favourable spawning areas.

7. Fate of Recently-hatched Fish

During the sampling period, recently-hatched G. vulgaris were observed in the quiet pools and backwaters of the River Glentui in late

FIGURE 22. One of two trap nets used in the present study. The frames were covered with 1 mm^2 mesh fabric netting and had the following dimensions: leader, 7 m x 1 m; wings, 1.3 m x 1 m; pot, 1.2 m x 30 cm x 30 cm; trap opening, 1 m x 1 m; funnel opening, 2.5 cm in diameter. This description was taken from Staples (1971 unpublished). (Photograph - P. C. Mason).

September, October and November. Stokell (1955) and Benzie (1961, unpublished; 1968d) reported finding recently-hatched G. vulgaris in similar situations. Since the eggs were laid in the riffle areas, the newly-hatched fish either swam upstream or moved downstream to the more quiet stretches where they are normally found. Two lines of evidence suggest that the latter is the case.

Firstly, trap nets (Fig. 22) were set at both the upstream and downstream limits of a riffle area known to contain egg masses in which the eggs were near the point of hatching. Thus, any fish moving either upstream or downstream from the riffle area would pass into the nets. The trap nets were left in position for 24 hours on two occasions, viz. 20,22-9-71 and 28,29-9-71; accumulation of debris prevented the nets from being set effectively for longer periods. At the first setting, no recently-hatched fish were found in either net. However, on the second occasion, although no recently-hatched fish were found in the upstream net, 37 were found in the downstream net.

TABLE 17. Ability of recently-hatched G. vulgaris, ranging in length from 10 to 14 mm, to maintain their position in currents of different velocities. Each fish was initially placed in the middle of the stream tank. (N = number of fish used in each set of conditions).

Water velocity at midpoint (cm/sec)	Water depth (cm)	Length of each trial (minutes)	N	position at the end of the trial		
				downstream	middle	upstream
9.1	10	10	20	1	12	7
11.4	10	10	20	5	9	6
15.9	10	10	24	15	9*	0
36.9	5	<1	18	18	0	0

* These fish were able to maintain their position only by remaining at the surface of the substrate.

Secondly, the current tolerance of recently-hatched fish was investigated in a small, closed-system, stream tank described by Craig (1966:70). The tank had a substrate of gravel and small boulders (<10 cm)

and the flow of water through the system was altered to obtain four different water velocities (measured at the midpoint of the tank using a Gurley No. 625 Pygmy Velocity Gauge). In October 1971 individual, recently-hatched fish, ranging in length from 10 to 14 mm, were introduced into the middle of the tank and the position of each fish was noted after a period of ten minutes; in some cases the trials lasted for less than one minute. Fish were recorded as having maintained their position in the middle of the tank, moved upstream or moved downstream. All fish were released into the tank from a small dipnet at the surface of the gravel. The results of these trials are presented in Table 17. When placed in the tank, all fish were positively rheotactic.

At low current velocities, most fish were able to maintain their position and some were able to swim upstream. At a higher current velocity (15.9 cm/sec) fish were able to maintain their position only by remaining at the surface of the gravel; as soon as they attempted to swim, they were swept downstream. At the highest current velocity which could be obtained in the experimental system (36.9 cm/sec), fish were swept downstream almost as soon as they were released into the tank. Since the lowest current velocity measured above a nest in the River Glentui was 46 cm/sec, it is evident that G. vulgaris after hatching are swept downstream.

Recently-hatched G. vulgaris are positively phototropic; this was indicated by their response to light in still-water aquaria, where all fish congregated in the illuminated sections. In the stream tank trials, the attempts of fish to reach the water surface increased the liklihood of them being swept downstream. The extent of the downstream movement in the River Glentui was not determined, but it was evident that movement ceased when a situation was reached where the recently-hatched fish were able to maintain their position and swim about freely in open water, without being swept further downstream. Thus, the downstream movement might cease immediately below the riffle in which the eggs were laid or at succeeding quiet stretches further downstream.

Downstream movement of recently-hatched fish has been reported for a number of stream-dwelling fish, e.g. paddlefish, Polydon spathula

(Purkett, 1961); red-finned bully, Gobiomorphus huttoni (McDowall, 1965a); Piute sculpin, Cottus beldingi (Sheldon, 1968); coastrange sculpin, Cottus aleuticus, and prickly sculpin, Cottus asper (McLarney, 1968). The phenomenon is widespread in the family Salmonidae and has been reported in whitefish, Coregonus laveratus (Fabricius and Lindroth, 1954), Salmo gairdneri (Northcote, 1962, 1969a), Salmo trutta (Kalleberg, 1958; Elliott, 1966), Salmo salar (Kalleberg, 1958), Oncorhynchus kisutch (McDonald, 1960; Chapman 1962), Oncorhynchus nerka, Oncorhynchus gorbuscha and Oncorhynchus keta (McDonald, 1960).

The downstream movement of some young fish may be attributed to intraspecific aggression (Kalleberg, 1958; Chapman, 1962; Le Cren, 1965; Mason and Chapman, 1965). In many cases the movement of recently-hatched fish results from passive displacement once the fish leave the protection of the nest site. Positive phototropism has been reported in a number of fish e.g. G. huttoni (McDowall, 1965a); when the larval fish swim upwards into the stream current they are carried downstream. Kalleberg (loc. cit.) indicated that downstream dispersal of S. salar and S. trutta may be caused by the fry swimming to the surface to fill their swimbladders with air. Diel periodicity has been demonstrated in the downstream drift of fry of S. trutta (Elliott, loc. cit.) and of C. beldingi (Sheldon, loc. cit.). In both species, movement occurred mainly at night and in S. trutta the onset of movement was correlated with sunset. Similarly, the downstream migration of sockeye, coho, pink and chum salmon fry was initially nocturnal and appeared to be regulated quite precisely by changes in light intensity. Downstream movement occurred as a result of displacement by the current when firm visual contact with objects in the stream was lost (McDonald, loc. cit.). Northcote (1962, 1969a) suggested that water temperature may be important in determining the response to water currents in fry of S. gairdneri, most of which move downstream soon after emergence.

In G. vulgaris, downstream movement of recently-hatched fish appeared to be a passive process. Although a number of factors, particularly temperature, may have affected the time of hatching, positive phototropism after hatching evidently caused the fish to swim upwards; once out of the nest they were carried downstream. This is a fate similar to that of recently-hatched G. maculatus. The eggs of this species

are laid amongst vegetation in the tidal reaches of rivers and streams. After hatching, the larvae are washed downstream and into the sea (Benzie, 1968a; McDowall 1968a, 1970). Pollard (1971) found a similar situation in a landlocked population of G. maculatus in Lake Modewarre, Australia. In this case eggs were deposited amongst flooded vegetation in streams flowing into the lake. After hatching the larvae were swept downstream into the lake. Again, the process appears to be a passive one. Recently-hatched fish are positively phototropic (Benzie, 1968a; Pollard, loc. cit.), so that once the fish swim out of the vegetation they are swept downstream. The life histories of other galaxiids are poorly understood, but it appears that the larvae of G. argenteus, G. fasciatus, G. postvectis and G. brevipinnis also move downstream. Spawning is thought to occur in the normal freshwater adult habitat, i.e. small bush creeks, streams and swamps, and juveniles migrate back into freshwater from the sea in the following year (McDowall, 1968a, 1970; Hopkins and McDowall, 1970). Thus, between the time of hatching and the return to freshwater as juveniles, there is a downstream movement of young fish to the sea. Here they have access to the prolific marine plankton. Similarly, in G. vulgaris which completes its life history in freshwater, downstream dispersal brings about a more efficient use of the space and food resources of the total available habitat, as was pointed out by Northcote (1967).

8. Discussion

Galaxias vulgaris was found to spawn in late winter and early spring. The onset of spawning appears to be temperature-dependent, so that spawning occurs first in the warmer parts of the river. Since changes in photoperiod are similar over the whole geographical range of G. vulgaris, temperature differences may explain the different spawning seasons reported by Benzie (1968d) and McDowall (1970). McDowall (loc. cit.) did not indicate the rivers from which his samples were taken, but Benzie (loc. cit.), working in the Cass River which is mainly snow fed, found that the spawning season of G. vulgaris occurred in spring and early summer. This is later than in the River Glentui which is not snow fed and consequently warmer than the Cass River. However, more detailed, simultaneous information is required on the spawning season and

environmental conditions in a number of rivers, before any definite conclusions can be made concerning the role of temperature on the spawning season of different populations of G. vulgaris.

There is no evidence of pair formation for the purpose of spawning, although spawning appears to some extent to be communal. From both field and laboratory observations it appears that males, probably in small groups, select and prepare the nest site(s) in the most turbulent parts of a riffle. Females, after making a few modifications to the nest, lay their eggs and then move away from the area, usually downstream. The aggressive behaviour of the males in particular, at this time of the year, is probably instrumental in chasing spent females from the nest site. It appears that more than one female may lay eggs in each nest and that each egg mass receives sperm from more than one male. An instance similar to this latter observation was reported in pike, Esox lucius, by Fabricius and Gustafson (1958), who found that most spawning groups consisted of 2-3 males and one female.

The attachment of males to the nest site is most probably related to the multiple shedding of sperm, rather than to any parental behaviour. Thus, males remain at the nest site until all their sperm has been shed or until the end of the spawning season, i.e. when there are no more ripe females, when the residual sperm is resorbed. This is indicated by the capture of partly spent males in October and November in the River Glentui, at a time when all females are spent. At the end of the spawning season, most of the unspent males are aged 0+, although many of these are partly spent. Of the males caught near nest sites in the River Glentui, only four out of 32 were aged 0+; three of these were still ripe, while one was partly spent. The behaviour of males just before spawning was not observed, but there is some evidence to indicate that groups of older males may chase age 0+ males from the nest site. The role of the age 0+ males at spawning appears, therefore, to be subsidiary to that of older males. A similar situation occurs in Salmo salar (Jones, 1959), the spawning of which shows a number of similarities to that of G. vulgaris.

In S. salar, ripe female parr are hardly ever found, while up

to 75% of the male parr may be ripe (Jones, loc. cit.). Spermatogenesis is normal in the male parr, the sperm of which has been used successfully to fertilize ripe ova and produce viable offspring. The role of the male parr at spawning was observed in a stream tank where it was found that they contributed sperm to the eggs laid in the redd, although the presence of an adult male was necessary to induce spawning by the female. Jones considers that the role of the male parr is an important one. Because of its size, the adult male may pass out sperm when its vent is about 10 cm above the bottom, so that its sperm may not reach the lowest eggs. Since the male parr are so small and are always at the bottom of the spawning bed, they are capable of fertilizing these eggs. Once the female has finished spawning, it moves downstream to a quiet pool. However, the male remains on the spawning bed. Jones considers that the adult males often spawn with more than one female and remain on the beds even when spent, apparently still with the urge to spawn. Here the male parr may play another important role, because if the almost spent adult male stimulates a female to shed eggs which it cannot fertilize, sperm may be provided by the parr. Since sexual activity persists in the males, the proportion of males to females on the spawning beds increases as the spawning season progresses. Thus, spawning beds of S. salar with an entirely male population have been reported (Menzies, 1925:44).

A number of the observations made by Jones may be pertinent to an understanding of spawning in G. vulgaris, males of which species persist at the spawning area. It has been suggested that multiple shedding of sperm occurs as in salmon. The size difference between age 0+ males and older males is much less in G. vulgaris than the difference between the parr and adults of S. salar, so that it is unlikely that age 0+ G. vulgaris males fertilize eggs which the sperm of older males cannot reach. However, it is possible that age 0+ males fertilize eggs laid late in the spawning season, at a time when most older males are spent. As pointed out by Jones for S. salar (1959:128), it may be that age 0+ G. vulgaris only play an important role in adverse conditions and, therefore, act as a form of insurance by significantly

increasing the proportion of potential-spawning males, ensuring that all eggs are fertilized.

Galaxias vulgaris was seen to behave aggressively towards similar sized P. breviceps and S. trutta in laboratory aquaria (see Chapter VII). Thus, although no distinct parental behaviour was observed, it is likely that the presence of the males at the nest site throughout the spawning period prevented both intraspecific and, to some extent, interspecific predation of eggs in the main egg mass, but this protection would not extend to any stray eggs swept downstream. No eggs were found in the stomachs of G. vulgaris in laboratory situations and only two fish taken from the River Glentui were found to have eaten eggs (see Chapter VI).

The relationship between egg size, number of eggs and life history in the New Zealand galaxiids has been discussed by Benzie (1968d) and McDowall (1970), who found that egg number and egg size were correlated with the life history pattern. Thus, the species with marine life history stages have numerous, small eggs, e.g. G. maculatus has up to 13,000 eggs (McDowall, 1968a) with a mean diameter (unfertilized) of 1.0 mm (Benzie, 1968c). Similarly, landlocked derivatives of G. maculatus (McDowall, 1970) and G. brevipinnis (Benzie, 1968d; McDowall, 1970), living in lakes, have numerous, small eggs. McDowall (1970) suggested that high larval mortality because of predation and dispersal, together with a plentiful food supply of plankton, has favoured selection for numerous small eggs in these species.

On the other hand, in the wholly freshwater, river-dwelling galaxiids there is a tendency towards fewer and larger eggs, e.g. G.vulgaris has 284-1,911 eggs (see section 3 of this Chapter) with a mean diameter of 1.36 mm. However, the length at hatching of G. vulgaris and G. maculatus is practically the same (7.2 mm (Benzie, 1968d) for G. vulgaris; between 6.6 mm (Benzie, 1968d) and 7.1 mm (McDowall, 1968a) for G. maculatus), although, on hatching, more yolk is present in the yolk sac of G. vulgaris than in that of G. maculatus, and G. vulgaris young are much more substantial than the young of G. maculatus (Benzie, 1968d). McDowall (1970) suggested that the food reserve is more important in species such as G. vulgaris in which the

larvae develop in running fresh water, giving the larvae a better chance of resisting downstream dispersal and also compensating "for any paucity of food available to very tiny fishes in rapidly flowing water". However, newly-hatched G. vulgaris are carried downstream soon after hatching and complete their early development in the quieter parts of the River where they have no difficulty in capturing food (see Chapter VI). Although the yolk reserves may be used before the larval fish become established in the quieter parts of the River, fish were found to feed on dipteran and ephemeropteran larvae before all their yolk had been absorbed. Similarly, Benzie (1968d) reported two-day-old G. vulgaris, still with half their yolk reserves, feeding on trichopteran larvae. Therefore, the size of the yolk reserves, as such, may not be as important for the survival of G. vulgaris as suggested by McDowall. Rather, it may be a by-product of a more precise system of reproduction in G. vulgaris than in the diadromous species such as G. maculatus, brought about by the occurrence of a definite nest site and a system of ensuring that most eggs are fertilized. It is evident that more eggs may be successfully fertilized when spawning occurs in a definite nest than when spawning occurs in flooded vegetation in the tidal reaches of a river, as in the case of G. maculatus. The chances of survival of fertilized eggs must also be greater in a well-situated nest. Thus, in G. vulgaris, since both the chance of fertilization and the survival of fertilized eggs are increased, a reduction in the number of eggs, with a corresponding increase in size, would be expected in comparison with G. maculatus which apparently does not make use of a nest. In G. divergens which has a few (145-252), large (2.0 mm before being laid) eggs, Hopkins (1971a) suggested that eggs were scattered by repeated deposition of small batches on different stones. Although the evidence for this is slender, if it occurred it would suggest that the relationship between spawning males and females is much closer than in G. maculatus and G. vulgaris and would suggest, therefore, an even more precise fertilization mechanism for G. divergens. A similar situation may occur also in G. paucispondylus and G. prognathus both of which have a few, large eggs. However, nothing is known of the spawning habits of these species.

Thus, the presence of fewer and larger eggs in G. vulgaris, compared with the diadromous species such as G. maculatus, is probably the result of a more precise fertilization process, with subsequent survival of more fertilized eggs. More information on the spawning behaviour of all the New Zealand galaxiids is required before this line of argument can be pursued.

Chapter V

HOME RANGE AND MOVEMENTS OF G. VULGARIS

Burt (1943) defined the home range of mammals with reference to the area normally covered in search of food. Later workers (e.g. Hayne, 1949, Gerking, 1953) extended the definition by omitting the "in search of food" part of it. In the present study, home range was used to refer to that part of the River Glentui normally covered by G. vulgaris in order to carry out its maintenance activities.

The concept of home range was first applied to stream fish by Gerking (1950, 1953, 1957, 1959) and a number of workers have shown that stream- and river-dwelling fish, in a wide variety of taxonomic groups, occupy a specific home range for long periods (see, for example, Shetter, D. H., 1937; Schuck, 1945; Scott, 1949; Allen, 1951; Sigler, 1951; Stefanich, 1951; Larimore, 1952; Funk, 1957; Miller, 1957; Gunning and Shoop, 1962, 1963, 1964; Gunning, 1963; McCleave, 1964; Stott, 1967; Edmunson, Everest and Chapman, 1968; Magnin and Beaulieu, 1968; Shetter, D. S., 1963; Burnet, 1969b; Munther, 1970). However, no information is available in the literature on the stability and home range of any of the New Zealand stream-dwelling galaxiids.

The present investigation was carried out in order to define the home range of G. vulgaris in the River Glentui and to follow any movements which might occur within the river. Galaxias maculatus is known to migrate to estuarine flats from its normal adult habitat, in small, stable lowland streams, for spawning purposes (Burnet, 1965; Benzie, 1968a; McDowall, 1968a, 1970). Although Stokell (1955) and Benzie (1968d) suggested that spawning in G. vulgaris occurred in the normal adult habitat, no evidence was provided to demonstrate that spawning of any particular group of fish took place in the same area which it occupied at other times of the year.

1. Methods

The investigation of home range was confined mainly to a 487 m stretch of the River Glentui (see Fig. 1). Fish from four adjacent sections were marked distinctly and their subsequent movements were followed by electric fishing at regular intervals.

TABLE 18. Length, width, depth and character of the sections regularly fished in the home range investigation. (1, 2, 3, 4 = the marking sections; D1 – D6 = sections downstream from the marking sections; U1 – U5 = sections upstream from the marking sections; R = riffle; Q = quiet stretch; CH = deep channel; P = deep pool; c = depth of channel in mainstream; s = depth of side pool; * indicates that the nature of the section changed from riffle to quiet stretch during the course of the study; velocity = mean water velocity 3 – 4 cm above the substrate, measured on 22–3–71).

Section	Length(m)	Width (m)									Depth (cm)									Velocity (cm/sec)	Section type
		April 1971			Nov. 1971			March 1972			April 1971			Nov. 1971			March 1972				
		Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean	Max.		
D6	8	–	–	–	–	3.7	–	–	2.4	–	–	–	–	–	7.3	–	–	11.0	–	–	R
D5	11	–	–	–	–	2.7	–	2.0	3.7	5.5	–	–	–	–	7.3	–	17.0	25.0	39.0^{S}	–	Q
D4	14	–	–	–	3.7	4.0	4.3	2.7	3.1	3.7	–	–	–	3.0	5.6	8.2	7.0	12.0	20.0	–	R
D3	12	–	–	–	–	2.7	–	–	2.1	–	–	–	–	–	5.5	–	–	11.0	–	–	Q
D2	35	3.1	4.0	5.2	3.4	3.9	5.2	2.3	2.9	3.7	6.0	15.4	40.0^{S}	17.0	19.3	21.0	10.0	12.0	15.0	–	R
D1	34	4.0	5.2	6.5	3.7	4.4	4.9	2.4	3.3	4.0	11.0	26.1	60.0^{S}	13.0	23.0	63.0^{S}	5.0	16.0	53.0^{C}	9.1	Q
1	35	2.0	4.3	7.0	2.4	3.7	5.8	2.1	3.1	5.3	4.0	19.2	42.0^{C}	24.0	27.8	48.0^{C}	12.0	17.0	42.0^{C}	26.5	R + CH
2	68	5.2	5.5	5.6	3.7	4.5	6.4	3.4	3.6	4.8	9.0	12.2	19.0	13.0	19.7	70.0	8.0	17.0	39.0	35.1	R*
3	38	5.8	7.2	8.9	2.7	5.3	7.0	2.4	5.9	9.5	4.0	10.7	17.0	10.0	17.0	39.0^{S}	6.0	12.0	28.0^{S}	41.8	R
P	12	4.3	6.2	8.8	–	–	–	–	7.0	–	38.0	56.0	72.0	–	–	–	18.0	31.0	35.0	0	P
4	24	4.0	4.1	4.2	3.4	4.7	5.5	4.3	4.6	4.9	12.0	16.0	23.0	13.0	19.3	27.0	9.0	11.5	14.0	37.2	R
U1	49	4.0	4.9	6.7	2.4	5.0	6.7	3.1	4.2	6.1	6.0	13.7	30.0	10.0	18.5	31.0	8.0	15.0	34.0	16.2	Q
U2	70	1.0	2.9	7.3	3.4	5.4	7.6	2.1	4.9	7.9	8.0	17.0	31.0	7.0	13.7	23.0	7.0	15.0	27.0	–	R + CH
U3	48	–	–	–	3.0	3.8	4.6	3.3	3.4	3.6	–	–	–	6.0	17.0	41.0^{S}	10.0	20.3	41.0^{S}	–	Q
U4	21	–	–	–	4.3	5.1	5.8	2.4	3.3	4.2	–	–	–	11.0	12.0	13.0	7.0	9.0	10.0	–	R + Q
U5	8	–	–	–	3.4	5.3	7.6	1.8	3.7	7.3	–	–	–	2.0	13.0	28.0	9.0	16.5	28.0	–	R + CH

FIGURE 23. Sections of the River Glentui regularly fished in the home range investigation, (see Table 18 for further details):

1. U4, part quiet, part riffle.
2. U3, quiet.
3. U2, riffle.
4. U1, quiet.
5. section 4, riffle.
6. pool.
7. section 3, riffle.
8. section 2, mainly riffle, part quiet.
9. section 1, riffle.
10. deep channel in section 1.
11. D1, quiet.
12. part of D1 where recently-hatched G. vulgaris were found.
13. D2, riffle.
14. D3, quiet.
15. D4, riffle.
16. D5 (foreground), quiet; and D6, riffle.

All photographs, except 10 and 12, were taken from the middle of each section, facing downstream.

1

5

2

6

3

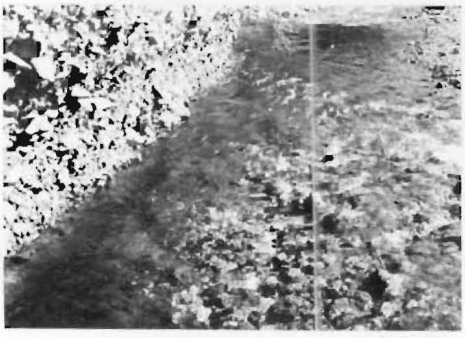
7

4

8

9

13



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11

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12

16

TABLE 19. Relative abundance of each fish species (A. australis and A. dieffenbachii combined) in each section regularly fished during the home range investigation. (0 = absent, 1 = present, but in small numbers, 2 = common, 3 = abundant, * = many young individuals after spawning season). (See Table 26 for population estimates of G. vulgaris in sections 1, 2, 3 and 4 combined).

	D6	D5	D4	D3	D2	D1	1	2	3	P	4	U1	U2	U3	U4	U5
G. vulgaris	1	0*	1	0*	2	1*	2	2	2	0*	2	1*	2	1	0*	2
P. breviceps	2	1*	2	1*	2	3*	2	3	2	2*	2	3*	2	2*	1*	2
S. trutta	0	0	1	0	2	0	2	1	2	1	1	2	2	1	0	1
Anguilla spp.	1	0	1	1	1	2	1	1	1	1	1	1	1	1	0	1

TABLE 20. Details of G. vulgaris marked in the home range investigation. (N = number of fish marked; TLs = total lengths of marked fish in mm).

Section	Date	Type of Mark	N	TLs Min.	TLs Mean	TLs Max.
1	9-3-71	Anal	21	52	74	112
	6-4-71	Anal & Caudal	30	56	78	110
2	9-3-71	Caudal	45	53	86	118
	7-4-71	Caudal & Dorsal	43	55	74	112
3	8-3-71	Dorsal	33	51	84	125
	7-4-71	Dorsal & Anal	22	58	72	105
4	8-3-71	Caudal, Dorsal & Anal	20	58	84	121
	8-4-71	Right Pectoral	15	53	78	106
1,2,3,4	March		119	51	82	125
1,2,3,4	April		110	53	76	112

The four sections in which fish were marked consisted of two riffles separated by a deep pool (< 72 cm deep). The larger, downstream riffle (141 m long) was arbitrarily divided into three sections (1, 2 and 3), whilst the smaller, upstream riffle (24 m long), together with the deep pool (12 m long), constituted the fourth section. The length, width, depth and character of these sections were recorded before, during and after the home range investigation and, together with similar data for adjacent sections both upstream (U1 - U5) and downstream (D1 - D6), are presented in Table 18; the nature of these sections is indicated also in Fig. 23. The relative numbers of each fish species in the River were estimated in each section and are presented in Table 19. These data refer to numbers and not to biomass, so that, although only a few eels were recorded in each section, they contributed substantially to the biomass of fish in the River. The presence of P. breviceps and S. trutta was shown to affect the distribution of G. vulgaris, and vice versa (see Chapter VII), so throughout the investigation, no fish of any species was removed from between sections D2 and U2. The number and range of total lengths of fish marked in each section, together with the types of marks used, are presented in Table 20. All marks were made with Alcian Blue dye using a jet inoculator (see Chapter I). A total of 229 fish were marked, 119 in March and 110 in April 1971. At this time of the year, the sexes could not be distinguished externally with any degree of certainty, so that the numbers of males and females marked were not known. However, the 1:1 sex ratio recorded in previous samples in the River Glentui (see Chapter IV), suggests that approximately equal numbers of males and females were marked.

The movements of marked fish were traced by electric fishing at intervals from the time of marking until February 1972. During each fishing, the whole stretch of the River from section D6 to section U5 was fished. On each of these occasions each section was fished twice, the second fishing following immediately after the completion of the first. After capture, the G. vulgaris from each section were kept in separate containers. Each fish was measured and the presence of any marks was recorded. A note was made of the reproductive condition of each fish, where possible, and then all fish were returned to the middle of the section

TABLE 21. Distribution of recaptured G. vulgaris, marked in March and April 1971.

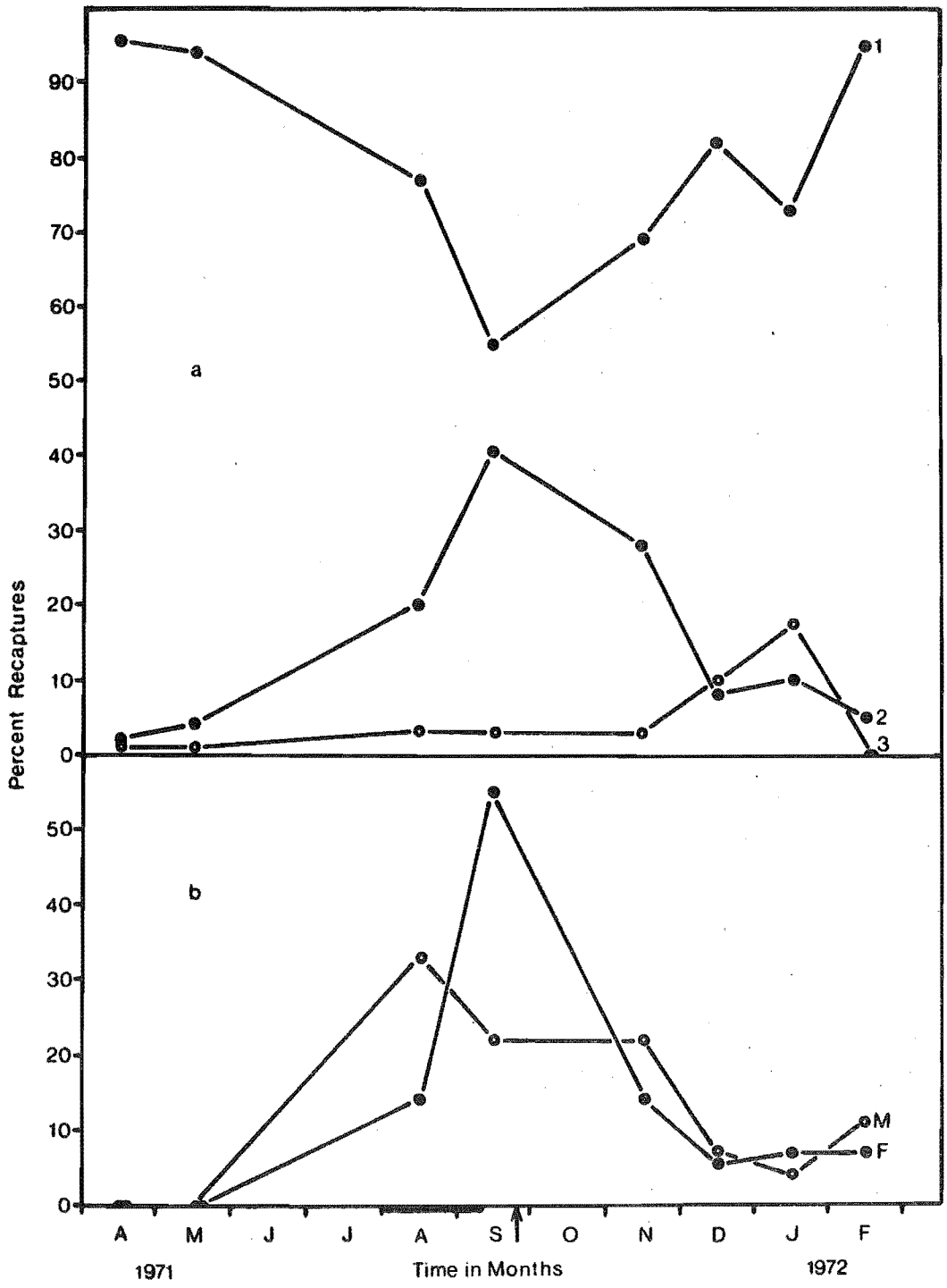
Section in which fish were originally marked	Sample date	Section of recapture															Total recaptures
		D6	D5	D4	D3	D2	D1	1	2	3	4	U1	U2	U3	U4	U5	>U5	
1	6,7,8-4-71							7	6	1								14
	3,4,5-5-71							13	1	2								16
	16,17,18-8-71			1				12	3				2					18
	21,22,26,28-9-71					1		5	1		1							8
	31-10;1,5-11-71					1		7			1		1				1	11
	20,22-12-71					2		9					1					12
	29,30-1-72					2		4										6
	26,27-2-72							3										3
2	6,7,8-4-71					1			18									19
	3,4,5-5-71					1			25	2	1							29
	16,17,18-8-71					1		3	11	4			2					21
	21,22,26,28-9-71							2	9	1	1		7			1		21
	31-10; 1,5-11-71							4	4	2			1					11
	20,22-12-71							7	5	4	1							17
	29,30-1-72				1			5	3	4				1		1		15
	26,27-2-72							3	3	7				1				14
3	6,7,8-4-71								2	15								17
	3,4,5-5-71								4	13	2							19
	16,17,18-8-71								1	11	2		3	2				19
	21,22,26,28-9-71								3	3	3		6					15
	31-10;1,5-11-71								3	2	1		2					8
	20,22-12-71					1		1	2	8								12
	29,30-1-72					1		1		4			1					7
	26,27-2-72								1	2								3
4	6,7,8-4-71										8							8
	3,4,5-5-71										4							4
	16,17,18-8-71										2		4					6
	21,22,26,28-9-71								1		5		8					14
	31-10;1,5-11-71										1	1	2	1		1		6
	20,22-12-71							1		1	4		2					8
	29,30-1-72										2							2
	26,27-2-72										1							1
																		384

FIGURE 24. a. Percentage of marked G. vulgaris in each sample recaptured in:

1. the section in which they were marked, or in adjacent sections,
2. further upstream,
3. further downstream.

Based on 884 recaptures.

b. Fish recaptured upstream from or in section U1. Recaptures of males (M) and females (F) are expressed as a percentage of the total number of males (n = 27) and females (n = 29) recaptured upstream from or in section U1. The shaded portion of the X-axis indicates the spawning season. The arrow indicates the time of the first appearance of recently-hatched fish.


Percent Recaptures
90
80
70
60
50
40
30
20
10
0
a
1
2
3
50
40
30
20
10
0
b
M
F
A
M
J
J
A
S
O
N
D
J
F
1971
Time in Months
1972

from which they had been taken. In addition to the above regular surveys, all samples of fish taken both upstream and downstream from the home range stretch of the River, (i.e. outside that part of the River extending from section U5 to section D6), were examined for the presence of marked fish. Any marked fish thus found were included in the results of the previous survey of the home range stretch.

2. Distribution of Recaptures and Size of Home Range

The number and distribution of all recaptures in each sample are presented in Table 21. Out of 384 recaptures, all, except 11, were taken in that part of the River between sections D2 and U2 inclusive, and all, except one, were taken between sections D4 and U5 inclusive. Only seven fish (1.8% of 384 recaptures) were recaptured in sections classified as quiet, all other fish were recaptured in riffle sections. Throughout the sampling period, no G. vulgaris, apart from recently-hatched fish, were found in the deep pool between sections 3 and 4.

It may be seen in Table 21 that the marked fish occupied a restricted portion of the River Glentui, with few fish moving far from the section in which they were marked. However, the proportion of fish recaptured in the section in which they were marked or in adjacent sections, and the proportion of fish moving further upstream or downstream varied throughout the sampling period. These data, for all sections combined, are presented in Fig. 24a. Since the sampling sections were defined arbitrarily, it was assumed that the home range of any particular fish may have overlapped adjacent sections. Thus, for the purposes of the present analysis, fish found in the sections immediately upstream and downstream from that in which they were marked were considered not to have moved. It may be seen in Fig. 24a that there were never less than 50% of marked fish in the section in which they were marked or in immediately adjacent sections. However, in August and September there was a sharp reduction in the number of fish found in these sections. This was correlated with an increase in the number of fish recaptured further upstream. The upstream movement occurred prior to spawning and indicated the movement of G. vulgaris to suitable spawning sites (see Chapter IV); no major downstream

TABLE 22. Distances moved by four fish recaptured one day after marking.

Section of marking	Date of marking	Section of recapture	Date of recapture	Distance moved(m)	Direction	Total length of fish (mm)
3	8-3-71	1	9-3-71	104.5	downstream	89
1	6-4-71	2	7-4-71	51.5	upstream	65, 109
1	6-4-71	3	7-4-71	104.5	upstream	92

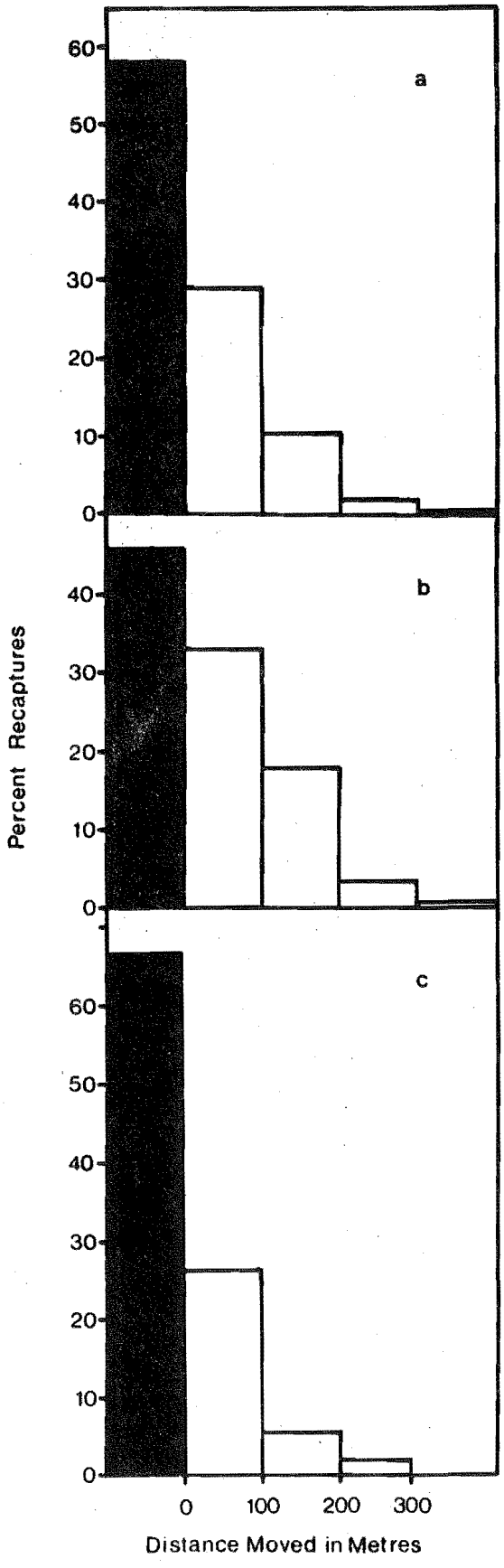
FIGURE 25. Proportion of G. vulgaris recaptured in the section of marking (shaded) and at 100 m intervals from it.

Key to letters:

a. Total recaptures, n = 384.

b. Recaptures in spawning season (Aug., Sept., Oct.-Nov.), n = 158.

c. Recaptures outside spawning season (April, May, Dec., Jan., Feb.), n = 226.


a
b
c
60
50
40
30
20
10
0
40
30
20
10
0
60
50
40
30
20
10
0
Percent Recaptures
0
100
200
300
Distance Moved in Metres

movement occurred. At this time of the year, all ripe fish, including those remaining in the section in which they were marked or in immediately adjacent sections, were found generally towards the head of the riffles. After spawning, the proportion of fish recaptured in the section in which they were marked, or in immediately adjacent sections, increased and the proportion of fish recaptured further upstream decreased.

In determining the distances travelled by fish recaptured in sections other than the section in which they were marked, measurements were made from the middle of the section of marking to the middle of the recapture section. The proportions of marked fish recaptured in the section of marking, and at 100 m intervals from it, are presented in Fig. 25a. Out of 384 recaptures over a period of 10-11 months, 87% were recaptured in the section of marking or within 100 m of it, whilst 97.4% were recaptured in the section of marking or within 200 m of it. Since batch marking was used in this investigation, no information was obtained on the minimum dimensions required for the home range of G. vulgaris. However, some fish were recaptured in the same 24 m stretch (section 4) 10-11 months after marking, indicating that the home range may be restricted to a rather limited section of the river.

The distances covered by four fish recaptured one day after marking (see Table 22) indicate that G. vulgaris is capable of moving relatively long distances during its life span.

3. Effect of Spawning on the Distribution of G. vulgaris

Reproduction, in many instances, occurred within the home range, but, in other instances, reproduction occurred upstream from the home range. Many stream- and river-dwelling fish have been shown to move upstream to spawn (see, for example, Lowe, 1964; Hynes, 1970a:349). As pointed out by Hynes (loc. cit.), this phenomenon is probably an important factor in the recolonization of depopulated areas.

In the present study, the proportion of marked fish recaptured in the section of marking and at 100 m intervals from it during the spawning period (August, September and October-November samples) and non-spawning period (April, May, December, January and February samples) are presented in Fig. 25.b,c. A comparison of the two distributions

using the G-test (Sokal and Rohlf, 1969:559) indicates that they are highly significantly different ($G = 54.815$, $d.f. = 4$, $p < 0.005$). Although a greater proportion of marked fish were recaptured further from the section of marking in the spawning period than in the non-spawning period, it may be seen in Fig. 25 that the actual distances travelled during the spawning period, in most cases, did not exceed the home range limits of G. vulgaris, i.e. the distances covered in the non-spawning period.

The extent of the upstream movement for spawning purposes is indicated by the number of marked fish recaptured in or upstream from section U1 (see Table 21), a 49 m stretch of the River, devoid of riffles, immediately upstream from the sections in which fish were marked. For the sampling period, the proportion of marked males and females recaptured in or upstream from section U1 (as percentages of all marked males ($n = 27$) and all marked females ($n = 29$) recaptured in or upstream from section U1, including four fish recaptured in March 1972 and combined with the February sample) are presented in Fig. 24b. Although the number of recaptures in this part of the river is relatively low, it is evident that males moved upstream earlier, and remained upstream longer than females. This further substantiates the roles of male and female at spawning, as indicated in Chapter IV, viz. males prepare the nest site(s) and show greater attachment to them than do females, which, after making some slight modifications to the nest, lay their eggs and then move downstream away from the nest site.

Only four immature marked fish (probably females) were recaptured above section U1 during the course of the study; three of these were recaptured in September and one in November, coinciding with the time of increased upstream recaptures of mature fish. This suggests that the factors affecting the upstream movement of mature fish may not be associated directly with the reproductive cycle.

Thus, in summary, prior to spawning there was a general upstream movement of G. vulgaris which, in some instances, extended beyond the home range limits.

4. Factors Controlling the Upstream Movement of G. vulgaris

The spawning migrations of G. maculatus were found to be correlated with lunar and tidal effects (see Chapter IV). In G. vulgaris,

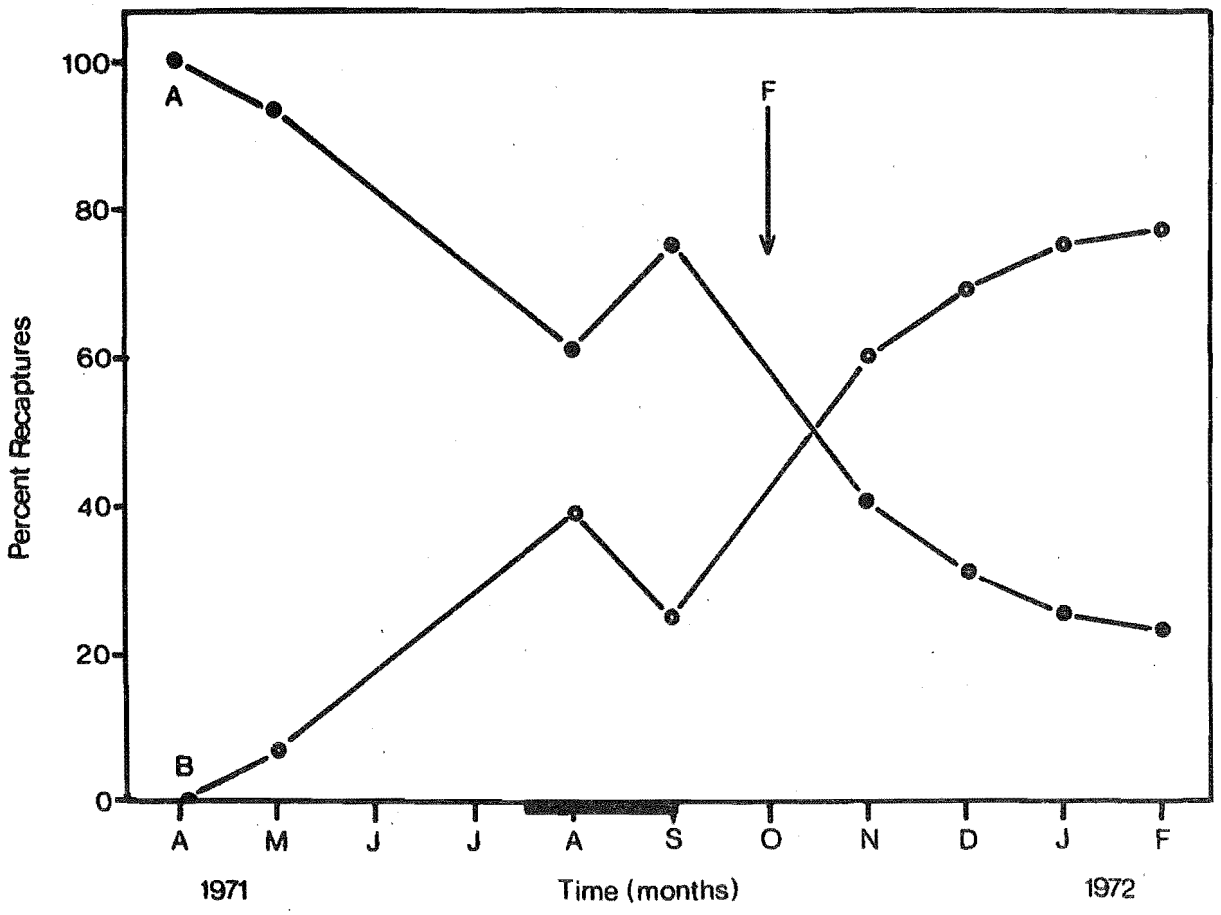
the onset of spawning was found to be correlated with temperature, spawning occurring first in the warmer parts of the River Glentui. Temperature, therefore, may play an important role in initiating upstream movement prior to spawning in G. vulgaris. In his review of the literature on the upstream migration of adult salmonids, Banks (1969) found that the rate of flow appeared to be the major environmental factor in most situations. Thus, an increased rate of migration generally was correlated with an increase in the rate of flow, although this relationship was subject to modification by light and temperature. Reduced flow, rather than increased flow, was correlated with the upstream spawning movement of G. vulgaris in the River Glentui, where spawning was found to occur at a time when rainfall is typically low (see Fig. 3c) and rate of flow is consequently reduced. In G. vulgaris the importance of physiological changes at this time of the year is indicated by a reversal of the normal diel activity pattern (see section 3 of Chapter VI). Hoar (1953) suggested that the timing and control of salmonid migration is mediated by neuro-endocrine processes, with the thyroid and gonadal hormones playing an important role, although other endocrine glands may also be involved. Baggerman (1957), working on the migration of the three-spined stickleback, Gasterosteus aculeatus, suggested that migration is caused by a delicate interaction between internal and external factors. Changes in the hypophysothyroid mechanism, brought about by both internal and external factors, were thought to be the primary cause of migration. Baggerman (loc. cit.) concluded that gonadal hormones do not play an essential role in the process, although they may have a modifying influence. More recently, Northcote (1969b) in his review of the lakeward migratory behaviour of juvenile rainbow trout, Salmo gairdneri, concluded that no single mechanism could explain the various patterns of migration observed in this species. In some instances, differences in migratory behaviour appeared to be induced mainly by environmental factors; in other instances, there appeared to be genetically controlled shifts in the thresholds at which the environmental factors operated, while, in some situations, there appeared to be a largely innate control. Similarly, Bjornn (1971) could not establish any consistent causal relationship between environmental factors and the migration of smolts of anadromous species of salmon and trout.

FIGURE 26. Proportion of G. vulgaris originally marked in section 2 and recaptured in:

A. The section of marking.

B. Adjacent sections, i.e. sections 1 and 3.

Based on 126 recaptures. (The shaded portion of the X-axis indicates the spawning season; the arrow indicates the time of the change in the nature of section 2, from riffle to pool.)


100
80
60
40
20
0
Percent Recaptures
A
B
F
A
M
J
J
A
S
O
N
D
J
F
1971
Time (months)
1972

Thus, the upstream movement of G. vulgaris probably depends on a number of different factors, both internal and external, any of which may assume a major role depending on the conditions prevailing at the time of the investigation.

5. Effect of Habitat Alteration on the Home Range of G. vulgaris

During the sampling period, the character of three of the marking sections, viz. sections 1, 3 and 4, remained essentially unchanged. However, following a heavy rainfall of 18.9 cm in October 1971, the nature of section 2 changed from mainly riffle to a pool-type habitat. This change was caused by the build-up of water and debris behind a fallen tree carried downstream by the flood waters and lodged in the lower part of the section. Evidently, the altered habitat was unsuitable for G. vulgaris which tended to move out of the quiet pool situation into riffle areas, both upstream (section 3) and downstream (section 1). This movement was indicated by the proportion of fish marked in section 2 and subsequently recaptured in the section of marking or in the two adjacent sections, viz. sections 1 and 3, (see Table 21 and Fig. 26). The reduction in the proportion of recaptures in section 2 in August and September was correlated with spawning. However, the reduction in the proportion of recaptures in section 2 from October onwards may be attributed to the changed nature of the section, since no similar situation was found in the other, three, unchanged sections. It may be seen in Fig. 26 that the reduction in the proportion of recaptures in section 2 corresponds with an increase in the proportion of recaptures in sections 1 and 3. Furthermore, there was no general downstream displacement as a result of the increased flow in October; from October onwards, fish from section 2 were recaptured in approximately equal numbers in section 1 ($n = 19$) and section 3 ($n = 17$). Thus, the movement of G. vulgaris from section 2 was not the direct result of increased water flow, but can be correlated with a modification to conditions in section 2 as a consequence of the increased water flow.

The ability of stream fish to withstand rapid increases in the rate of water flow following heavy rainfall is perhaps explained, in part, by an observation made by Stegman and Minckley (1959), who found three species of fish in the interstices of gravel 5-7 cm below the

surface of the stream substrate. All three species are usually found beneath rocks and other cover in riffles - a similar habitat to that of G. vulgaris. Also, G. vulgaris uses its outspread pectoral fins as hydrofoils to maintain its position when at rest on the river bed; the fins are held with their leading edge facing downwards and into the current, so that the fish is pressed against the substrate. A similar mechanism has been reported in other, active, stream-dwelling fish (see Hynes, 1970a:305).

6. Effects of Displacement

(1) Homing in stream fish and its sensory basis

For stream fish, homing has been defined as the return to a home range (Gunning, 1963). This return may follow a movement away from the home range for spawning, or it may follow natural or artificial displacement. Thus, this definition is distinct from that applied to anadromous fish in which homing refers to a return to the parent stream. However, both definitions may be included in Gerking's (1959) more general definition in which homing refers to "the choice that a fish makes between returning to a place formerly occupied instead of going to other equally probable places". The definitions of both Gerking and Gunning are applicable to the present investigation.

Homing has been demonstrated in a variety of stream-dwelling fish, excluding catadromous and anadromous forms. Schuck (1945) demonstrated that Salmo fario moved upstream to spawn and later returned to its home range. A similar situation was reported for brook trout, Salvelinus fontinalis, by Shetter (1937). Smallmouth black bass, Micropterus dolomieui, returned to their home pool when displaced experimentally between 1 and 1.4 km both upstream and downstream (Larimore, 1952). Also, Gerking (1953) and Gunning (1959, 1963) demonstrated that longear sunfish, Lepomis megalotis, returned to their home range after experimental displacement. Miller (1954), working with cutthroat trout, Salmo clarkii, reported an experiment in which a 0.8 km portion of a stream was screened off, and into the enclosure so formed, tagged trout were transferred from both upstream and downstream. When the screens were removed, trout of upstream origin, confined for less than 30 days, moved towards their original home; trout of down-

stream origin, confined for less than 30 days, showed less ability to move towards their original home. However, trout confined for more than 30 days tended to remain in the originally enclosed area, apparently having "adjusted to new homes." Stott, Elsdon and Johnston (1963) displaced 1,022 gudgeon, Gobio gobio, both upstream and downstream, in the River Mole. Of the 192 recaptures, 107 were taken in their original sections 15 to 23 days later. These examples of homing in stream fish, together with the more spectacular feats of the anadromous salmonids (see Jones, 1959; Hasler, 1960; Harden Jones, 1968; Sato, Omori and Maiwa, 1968), indicate that fish are able to return to a particular area and, once there, to recognize it as distinct from other areas.

Work by Donaldson and Allen (1958) and Zarnecki (1968) indicates that homing is due not to genetic factors, but to some type of imprinting by environmental factors. Donaldson and Allen (loc. cit.) switched stocks of coho salmon, Oncorhynchus kisutch, so that the eggs developed in different waters. When the adults returned from the sea, they did not return to their parent stream, but to the stream in which the eggs had hatched and in which they had lived as fry. Zarnecki (loc. cit.) found a similar situation in sea trout, S. trutta. The concept of imprinting as the basis for homing was first put forward by Hasler and Wisby (1951) who, referring to anadromous salmonids, proposed a hypothesis of homing based on a conditioned olfactory response to properties of the water of the parent stream (under natural conditions). However, Brannon (1967) produced evidence to show that genetic factors are responsible for the lakeward migration of the fry of sockeye salmon, O. nerka. Eggs from a stock that normally migrates upstream and eggs from a downstream-migrating stock were reared under identical conditions. The fry showed strong tendencies to swim in the same direction as their parents, with 80% of the experimentally reared fish choosing the direction characteristic of their stock when faced with an upstream-downstream choice. Hybrids showed intermediate behaviour.

The sensory mechanisms whereby a fish recognizes its home range were summarized by Harden Jones (1968). Within the home range, topographical features may be recognized visually, by tactile stimuli, by

means of the lateral line system, or, in some instances, by their effect on electric fields. The chemical nature of the environment is extremely relevant in relation to homing and recognition of the home range. Hasler and Wisby (1951) demonstrated the ability of bluntnose minnows, Hyborhynchus (= Pimephales) notatus, to discriminate between the waters of two chemically different creeks by means of olfactory cues. Furthermore, it was found that minnows, which do not undergo long migrations, could differentiate between the odours for a comparatively long period after the end of training. Collins (1952) showed that water temperature and the amount of free carbon dioxide influenced the orientation of alewives (Pomolobus).

Evidence for the role of the various sensory modalities used by fish returning to their home range or, in the case of anadromous salmonids, to their parent stream, has come mainly from experiments in which sense organs or their nerves have been removed or otherwise rendered ineffective. Such experiments invariably indicate that olfaction plays an important role in the location of the home range or parent stream (see, for example, Wisby and Hasler, 1954; Gunning, 1959; Groves, Collins and Trefethen, 1968; Kleerekoper, 1969:131; Jahn, 1969; LaBar, 1971). The work of Oshima, Hahn and Gorbman (1969a, b) indicated that homing quinnat, O. tschawytscha and coho salmon, O. kisutch, appeared to respond to individual loci along the route. This conclusion followed experiments in which various natural waters were infused into the nasal sacs of homing fish and recordings made of the electroencephalographic patterns from the olfactory bulb.

The substance(s) responsible for the olfactory response of homing fish is unknown, although it is known to be volatile and heat-labile (Hasler and Wisby, 1951; Idler et al, 1961). However, Nordeng (1971), working with char, Salvelinus alpinus, recently suggested that the local orientation of anadromous fish may be determined by pheromones.

Thus, the olfactory nature of the home range or parent stream appears to be the major factor affecting the orientation of stream fish and anadromous salmonids (notwithstanding the possible use of celestial or geophysical clues by salmonids at sea). In this respect, the increased rate of flow which generally results in an increased rate of upstream

TABLE 23. Details of fish used in displacement experiments.

	Group	Initial section	Displacement section	Distance displaced(m)	Number of fish	TL range Min.	Mean	Max.	Mark used
Expt. 1	1	3	3	0	8	55	87	113	left pectoral
	2	3	U2	139	8	57	83	99	right pelvic
	3	3	D2	173.5	8	73	90	117	left pelvic
Expt. 2	1	D2	D2	0	8	66	94	110	left & right pectoral
	2	D2	1	69	8	64	86	105	left pectoral, left pelvic
	3	1	D2	69	12	58	83	117	left pectoral, right pelvic

TABLE 24. The number and distribution of marked fish recaptured in the displacement experiments.

	Group	Number of recaptures	Distribution of recaptures																
			>U5	U5	U4	U3	U2	U1	4	3	2	1	D1	D2	D3	D4	D5	D6	< D6
Expt. 1	1	5	-	-	-	-	-	-	-	5	-	-	-	-	-	-	-	-	-
	2	3	1	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-
	3	5	-	-	-	-	-	-	-	-	-	1	-	4	-	-	-	-	-

	Group	Number of recaptures	Distribution of recaptures				
			upstream trap	1	D1	D2	downstream trap
Expt. 2	1	5	-	-	-	5	-
	2	2	2	-	-	-	-
	3	6	-	4	-	2	-

migration in adult salmonids (Banks, 1969) may be the result of an increased olfactory stimulation received by the fish, rather than a direct result of the increased rate of flow.

(2) Artificial displacement of G. vulgaris

Galaxias vulgaris was found to occupy a home range in the River Glentui. Although individual fish were not recognized, it may be inferred from the distribution of recaptures that those fish which moved beyond the limits of the home range for spawning purposes returned to their home range after spawning. In February and March 1972, two experiments of a preliminary nature were carried out to examine the effects on G. vulgaris of artificial displacement, both upstream, and downstream.

Experiment 1

On 27-2-72, 24 G. vulgaris were taken from section 3 and divided into three groups, each of eight fish. The fish in each group were marked distinctly: the marks used and the range of total lengths of the fish marked in each group are presented in Table 23. One group was then returned to the middle of section 3, another group was displaced 139 m upstream to the middle of section U2 and the third group was displaced 173.5 m downstream to the middle of section D2. Displacement distances were measured between the midpoints of the capture and release sections. On 4,5-3-72, the River was fished from 50 m downstream of section D6 through to section U5 and, on 7-3-72, a further 330 m stretch, immediately upstream from section U5, was fished. The number and distribution of marked fish recaptured during these fishings are presented in Table 24.

Experiment 2

On 30-3-72, a trap net (see Fig. 22) was set at the upstream end of section 1, facing downstream and another was set at the downstream end of section D2, facing upstream. A total of 16 fish was taken from section D2 and divided into two groups, each of eight fish. The fish in each group were marked distinctly and then one group was replaced in the middle of section D2 and the other group was displaced 69 m upstream to the middle of section 1. Before this latter group was released, a further group of 12 fish was taken from section 1, marked distinctly and displaced 69 m downstream to the middle of section D2. As in the first

experiment, displacement distances were measured between the mid-points of the capture and release sections. Details of the marks used and the range of total lengths of fish marked in each group are presented in Table 23. The design of this experiment was essentially the same as that of experiment 1, except that the trap nets were used in an attempt to catch any fish moving out of the experimental stretch of the River. On 1-4-72, one day later, sections D2, D1 and 1 were fished and the trap nets were examined for the presence of any marked fish. The number and distribution of recaptures are presented in Table 24.

(3) Discussion

It may be seen in Table 24, from the results of both experiments, that all recaptured control fish were taken in their original section. Of the 11 recaptures of downstream-displaced fish, six remained in the section of release and five moved back upstream, four returning to their original section. The distribution of recaptures of upstream-displaced fish indicated that most had moved further upstream. The results of these experiments suggest that some factors, probably olfactorily recognized, are carried downstream by the water current. Although six of the downstream-displaced fish remained in the section of release, it is possible that as far as chemical stimulation was concerned, they were still at "home", i.e. they were still receiving sufficient stimuli from further upstream to offset the distance displaced. Fish displaced upstream received no such stimuli from their original home range and were thus disorientated. For these fish, the search for the home range appears to have taken place in an upstream direction. This is indicated by one fish in experiment 1 recaptured 300 m upstream from the section of release and the two fish recaptured in the upstream trap net in experiment 2. In both experiments, no upstream-displaced fish were found in the section of release. The low level of recaptures of upstream-displaced fish probably reflects upstream movement out of the sampling area. The two exceptions in experiment 1, i.e. the two fish recaptured in sections 3 and 4, which were also the two largest fish in group 2, may have returned by random movement, or the release section (U2), may have been part of their range of experience as a result of a previous upstream movement for spawning. Again, the recapture of a fish in the section

adjacent to the original section may have been the result of a reaction by the fish to sufficient appropriate stimuli in that section.

Thus, from these limited observations, it appears that some clue carried downstream by the water current enabled fish displaced downstream to recognize their relative position. This clue was not available to fish displaced upstream, unless the distance of displacement fell within the range of their experience. Fish moving upstream to spawn, either must receive new stimuli which increase their experience and enable them to return to their home range after spawning, or a behavioural change after spawning causes the fish to move downstream until they receive familiar stimuli from their home range. In artificial upstream displacement, no information concerning the chemical nature of the part of the River between the sections of origin and release is obtained by the fish. Further work is required to test these ideas, but it appears that G. vulgaris, when displaced, responds to an overall stimulus, probably chemical in nature and olfactorily mediated, rather than to specific landmarks, although the latter may be of importance within the home range.

The greater success of downstream-displaced fish than upstream-displaced fish in returning to their original section or, at least, appearing less disorientated, is in line with the results obtained in similar experiments performed by Miller (1954), Gunning (1959, 1963) and Stott et al (1963). In the experiments of Stott et al (loc. cit.), the fact that only a proportion of the displaced fish homed was thought to be because the gudgeon population consisted of some individuals which were attached to a home range and some which were not. However, the distribution of recaptured gudgeon (see Table III in Stott et al, loc. cit.) may also be explained by assuming that those fish which did not home were receiving sufficient, appropriate stimuli in the section of recapture. Indeed, some gudgeon may not even have been displaced from their home range; no information was given concerning the size of the home range of gudgeon over a period of a year, although Lusk (1963, in Stott, 1967) indicated that it was quite extensive. Further field and laboratory experiments were carried out on gudgeon and roach, Rutilus rutilus (Stott, 1967).

Again, however, without a knowledge of the home range of these species over a period of at least one year, the interpretation of the results is open to question.

A number of other workers (e.g. Scott, 1949; Funk, 1957; McFadden, 1961; Logan, 1963; Behmer, 1964) have found a few marked fish far upstream or downstream from where they were originally caught, although most fish were recaptured in the original capture section. Thus, it appears that in these populations there were two groups, one, consisting of most fish, which was sedentary and another, consisting of few fish, which was mobile. The significance of the two groups is in doubt although Hynes (1970a:344) has suggested that they may be a means of dispersal of the species, even if they have little effect on the population as a whole. Scott (loc. cit.) considered that the small number of individuals recaptured far outside the normal range were aberrant. He based this conclusion on the type of tag carried by these fish; only the fish with a particular type of jaw-tag were found outside the normal range.

A further complication in such mark-recapture studies arises from the method of release after marking. In most experiments, as in the present study, fish are released in the middle of the section of capture; this section is usually arbitrarily defined. Thus, in the present study, for example, any fish with a home range extending from section 1 to the downstream part of section 2, may be caught in section 2 and, after marking, released in the middle of section 2, upstream from its normal range. In such instances, it is conceivable that released fish may behave as fish artificially displaced upstream and become disorientated, moving long distances further upstream in search of their home range. Such movements would seriously affect any interpretation of the distribution of subsequent recaptures.

7. The Fate of Juvenile G. vulgaris

Recently-hatched fish were shown to move downstream from the spawning sites in riffles to the more quiet stretches of the River (Chapter IV). Juvenile G. vulgaris were first caught in the normal adult habitat, in riffles, in late December and by mid-autumn (April) most age 0+ fish had moved out of the quiet stretches. No field evidence was obtained on the direction of movement of juvenile G. vulgaris on leaving

the quiet stretches. This was due mainly to the failure in finding a suitable marking technique for fish below 50 mm in total length. However, laboratory evidence indicates that this movement occurs in an upstream direction. In January 1972, using the stream tank in which the current tolerance of recently-hatched fish was investigated (see Chapter IV), it was found that as G. vulgaris increased in size they were able to maintain their position in the fastest experimental current (36.9 cm/sec; depth < 5 cm) and to swim upstream. In all trials conducted on individual fish between 24-41 mm in total length (n = 47), fish were found, after a period of five minutes, to be either at the release point, in the middle third of the stream tank (n = 13), or in the upstream third of the stream tank (n = 34): no fish were found in the downstream third. All fish were positively rheotactic. These results, together with the results of the trials with recently-hatched fish (see Chapter IV), suggest that age 0+ G. vulgaris, after initial downstream displacement, move upstream into the normal adult habitat.

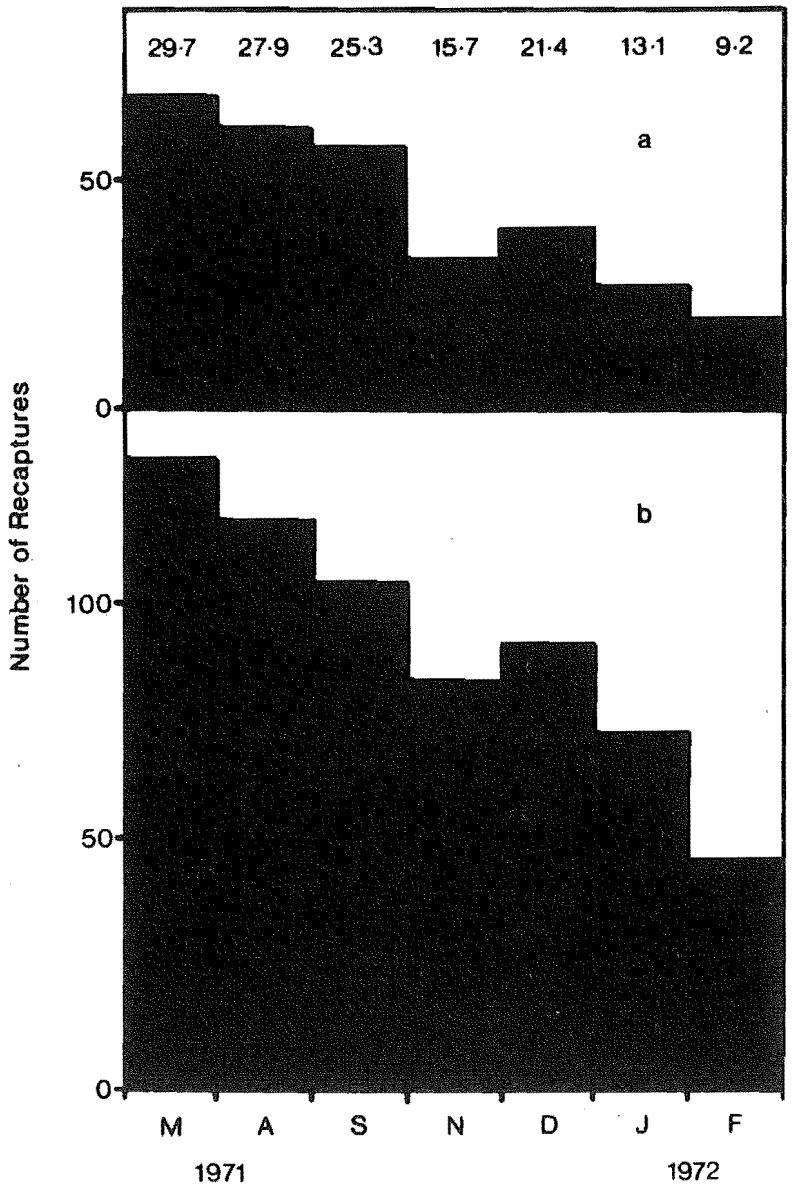
The movement from the quiet stretches into the riffles is associated with a number of behavioural changes. There is a change from a shoaling open-water existence to the more solitary, cryptic way of life of the adults. It is a time of physiological adjustment and coincides with the deposition of a secondary ring in the otoliths (see Chapter III) and a change in the growth pattern of the brain (see Chapter VI). The timing of the movement from the quiet stretches, as in the timing of the upstream spawning movement of the adults, probably depends on a complex interaction of internal and external factors. Rate of growth and the attainment of a certain critical size are no doubt important factors in this respect.

8. The Cause of the Reduction in the Number of Recaptures with Time

As pointed out by Harden Jones (1968:252), a weakness in most mark-recapture experiments concerned with home range and homing in fish is that most of the marked or tagged fish are not recaptured. Those fish which are recaptured provide good evidence for homing and the existence of a home range, but there must be some doubt concerning the whereabouts of fish not recaptured: these fish may have strayed, be at

FIGURE 27. a. Total number of marked G. vulgaris recaptured in samples taken between May 1971 and February 1972. The figures above the histogram represent the number of recaptures as a percentage of the number of fish originally marked (n = 229).

b. The number of unmarked G. vulgaris taken between sections D2 and U2 from May 1971 to February 1972. Age 0+ fish produced in the spawning season of 1971 are not included.


29·7
27·9
25·3
15·7
21·4
13·1
9·2
a
b
50
0
100
50
0
Number of Recaptures
M
A
S
N
D
J
F
1971
1972

home or be dead. The design of an experiment to investigate home range and homing must be such that all water potentially available to the marked fish is sampled. In all experiments, except those carried out in small lakes and ponds, this is not usually practicable. Also, careful consideration must be given to the choice of a suitable mark or tag (Rounsefell and Kask, 1945; Ricker, 1956), since inappropriate tags may lead to abnormal behaviour on the part of the fish (e.g. Scott, 1949). In the present study the marking technique and the mark itself were considered not to affect the behaviour of the fish (see Chapter I).

In the present study the proportion of marked fish recaptured, excluding those recaptured in April (when only the fish marked in March were available for recapture), ranged from 29.7% in May 1971 to 9.2% in February 1972 (see Fig. 27a). This decline in the number of recaptures may be explained by natural mortality, mortality caused by the marking technique, or movement out of the sampling area.

The number of marked fish caught in different parts of the River Glentui during the home range investigation, together with the number of unmarked fish caught during the same period, is presented in Table 25.

TABLE 25. Number of G. vulgaris caught in different parts of the River Glentui during the home range investigation, from April 1971 to February 1972. (This table does not include age 0+ fish produced in the 1971 spawning season). (Figures in parenthesis are percentages of total recaptures).

Area sampled	Fish caught		
	unmarked	marked	
D2 - U2*	912	373	(97.1)
D6 - U5** (excluding D2 - U2)	287	10	(2.6)
downstream from D6 & upstream from U5***	1,250 - 1,300	1	(0.3)

* All fish taken in samples in these sections were returned to the River.

** Most fish taken in samples in these sections were returned to the River.

*** Most fish taken in samples in these sections were not returned to the River.

It may be seen that although more than 1,250 G. vulgaris were caught in the part of the River outside the experimental home range stretch, i.e. outside that part of the River between sections D6 and U5, only one marked fish was found. The fish caught outside the home range stretch included 605 taken in April and May 1971 (for studies of population parameters); 402 taken from August to October 1971 (for reproduction studies); 168 taken in November 1971 (for food studies) and others taken for laboratory experiments throughout the home range investigation. The sites at which these samples were taken ranged from immediately below (and in one instance above) the most downstream waterfall (height = 2.5 m) to the upstream edge of section U5 (b-e in Fig. 1), and from the downstream edge of section D6 to the point where the River Glentui enters the River Ashley (f-g in Fig. 1). The waterfall was considered to be an effective barrier to any further upstream movement of fish, but the possibility of marked fish moving downstream into the River Ashley could not be ruled out. However, judging from the relative proportions of marked and unmarked fish recaptured in different parts of the River Glentui, it is assumed that no significant number of marked fish moved out of the experimental home range stretch of the River.

The decline in the number of recaptures throughout the sampling period is shown in Fig. 27a. A similar decline (see Fig. 27b) occurred in the number of unmarked fish caught between sections D2 and U2, from where no fish were removed during the course of the home range investigation, (all fish were returned to the River after they had been checked for marks). In November 1971, fishing efficiency was below normal because of flood conditions following heavy rainfall. This was reflected in both the total number of recaptures and the number of unmarked fish caught between sections D2 and U2. For the seven regular samples taken during the home range study, from May 1971 to February 1972, the product-moment correlation coefficient (Sokal and Rohlf, 1969:498) between the total number of recaptures and the number of unmarked fish caught between sections D2 and U2 was 0.9806 (95% confidence limits = 0.8701 and 0.9972) indicating that the proportion of marked to unmarked fish remained constant throughout

the sampling period. This suggests that the decline in the number of recaptures was due to natural mortality rather than to any long-term mortality caused by the marking technique.

9. Estimation of Population Number

The number of recaptures was used as a basis to estimate the population number of G. vulgaris throughout the sampling period. Data for sections 1, 2, 3 and 4 (the marking area) were combined for this purpose and the population estimates were based on the total number of recaptures. Although marked fish were shown to move out of the marking area, particularly during the spawning season, a correction factor to adjust for emigration was not applied. Such an adjustment is applicable only when there is no immigration of unmarked fish. In the River Glentui, it was assumed that any movement of marked fish out of the marking area was compensated for by an immigration of unmarked fish, e.g. the number of marked fish moving upstream from the marking area to spawn was assumed to be balanced by a similar upstream movement of unmarked fish into the experimental area.

TABLE 26. Population estimates of G. vulgaris in the marking area (sections 1, 2, 3 and 4) during the home range investigation. (m = total number of marked fish in the population; c = number of fish in the sample; r = number of marked fish recaptured; $\hat{N}$ = population estimate; S.E. ($\hat{N}$) = standard error of the estimate; the number of G. vulgaris/m^2 is based on a total area of 775.5 m^2 (length = 165 m, mean width during study = c 4.7 m))

Sample	m	c	r	$\hat{N}$	$\pm$S.E.($\hat{N}$)	G. vulgaris/m^2
6,7,8-4-71	119	167	58	342.6	26.0	0.4
3,4,5-5-71	229*	114	68	383.9	24.8	0.5
16,17,18-8-71	228	109	64	388.3	26.5	0.5
21,22,26,28-9-71	228	71	58	279.1	13.6	0.4
31-10; 1,5-11-71	228	66	36	418.0	43.2	0.5
20,22-12-71	228	95	49	442.0	39.0	0.6
29,30-1-72	228	59	30	448.4	53.5	0.6
26,27-2-72	228	43	21	466.9	69.5	0.6

* one marked fish died in this sample

The population number in the marking area at the time of each sample was estimated using the formula (Robson and Regier, 1968):

$$\hat{N} = \frac{mc}{r}$$

where $\hat{N}$ is the estimate of the total number of fish in the marking area, m is the total number of marked fish in the population, c is the number of fish in the sample and r is the number of marked fish recaptured. The standard error of the estimate, represented as S.E. $(\hat{N})$, was derived from the formula (Robson and Regier, loc. cit.):

$$S.E.(\hat{N}) = \hat{N}\sqrt{\frac{(\hat{N} - m)(\hat{N} - c)}{mc(\hat{N} - 1)}}$$

For each sample taken during the home range investigation, the population estimate for the marking area, together with the standard error of the estimate, is presented in Table 26. The estimates include all age groups present in the river in April 1971; they do not include young-of-the-year fish (recognizable by means of length frequency analysis) produced during the spawning season of 1971.

10. Conclusions

The distribution of marked fish recaptured from April 1971 to February 1972 indicates that G. vulgaris occupies a home range in the River Glentui. The stability of the population is indicated further by the different rates of growth found in different parts of the River (see Chapter III). Altered conditions may cause G. vulgaris to modify its home range, but this involves merely a movement into suitable adjacent areas. However, upstream movement out of the home range may occur during the spawning season. A summary of the movements of G. vulgaris in the River Glentui during the course of the present study is presented in Fig. 28. A similar situation was reported by Taylor (quoted in Northcote, 1967) for the sculpin, Cottus asper. In this species, the fry, shortly after emergence, move downstream to rich feeding areas near or at the estuary and then later as juveniles return upstream. This situation is probably widespread in stream-dwelling fish. Many species have been shown to move upstream to spawn and many have young stages which move downstream soon after hatching. Such a life cycle enables

FIGURE 28. Summary of movements of G. vulgaris in the River Glentui.

Key:

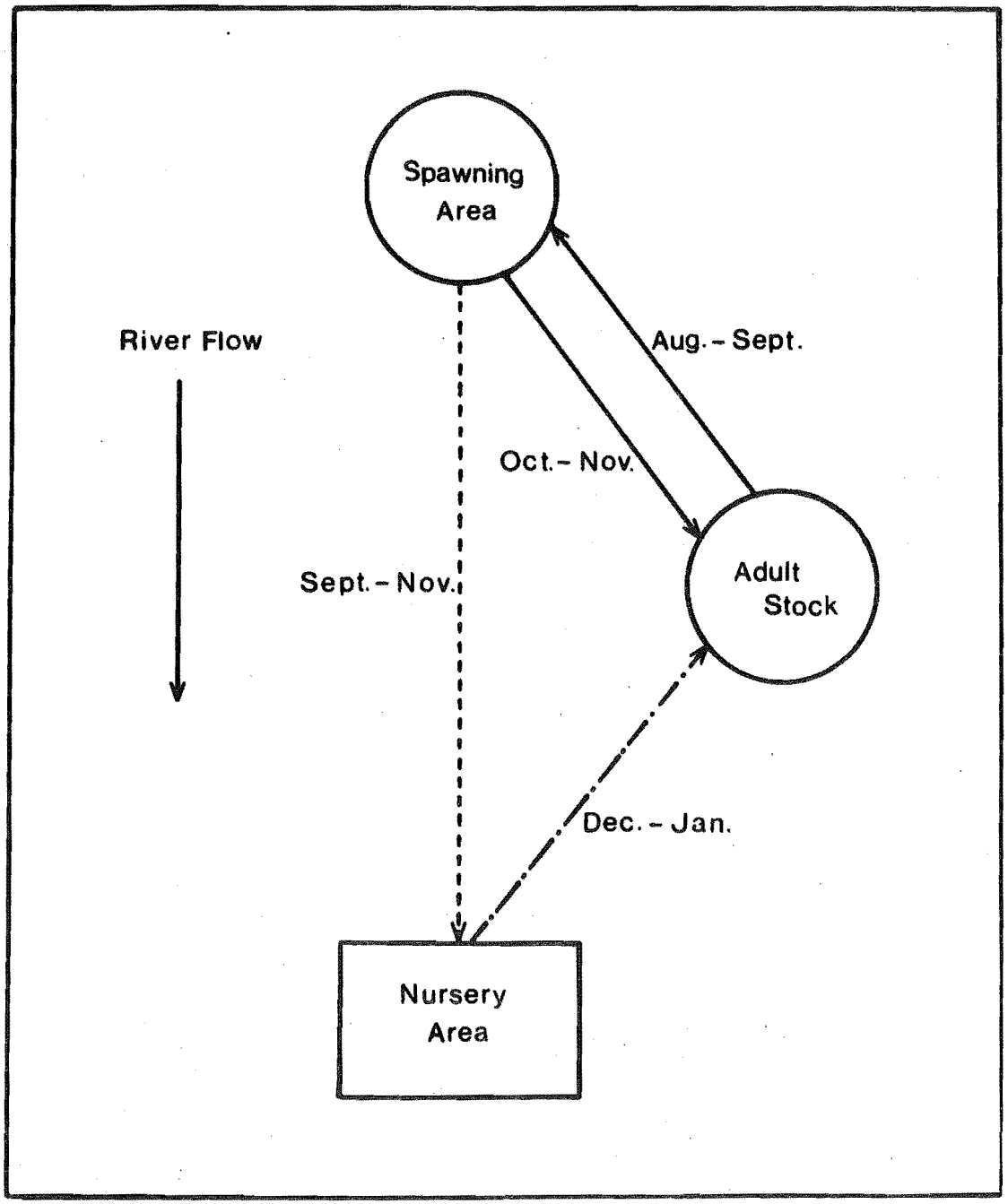
Circles denote riffle areas.

The rectangle denotes a quiet stretch of the River.

———— = Based on evidence from recaptured marked fish.

- - - - - = Based on trap-net and laboratory evidence.

——·—— = The direction of this movement is based on laboratory evidence only.


Spawning Area
River Flow
Aug. - Sept.
Oct. - Nov.
Sept. - Nov.
Adult Stock
Dec. - Jan.
Nursery Area

efficient use of the total available habitat.

The distances over which G. vulgaris is capable of moving in one day indicate that lack of mobility is not the factor which restricts it to a particular home range. Evidence suggests that some general chemical cue is responsible for the maintenance of the home range throughout the greater part of the life cycle.

Chapter VI

FOOD HABITS AND FEEDING MECHANISMS

The aims of this part of the study were, firstly, to examine the diet of G. vulgaris with respect to season, sex, size and age and, secondly, to investigate the feeding relationships of all the fish species inhabiting the River Glentui.

Little attention has been paid to the feeding habits of the New Zealand Galaxiidae, with the exceptions of G. maculatus (McDowall, 1968a) and G. divergens (Hopkins, 1971a), though work on introduced salmonids has usually included some information on the diet of cohabiting galaxiids (e.g. see Allen, 1951; Lane, 1964). Stokell (1949) stated that the food of adult G. vulgaris consisted of chironomid, ephemeropteran and trichopteran larvae, whilst Benzie (1968d) suggested that G. vulgaris fed on debris and insects washed downstream.

1. General Methods

(1) Collection of data

The analysis of the food habits of the fish in the River Glentui was based on an examination of the contents of 1,552 stomachs removed from fish sampled between June 1970 and November 1971 (G. vulgaris, n = 924; P. breviceps, n = 430; S. trutta, n = 98; Anguilla spp., (A. dieffenbachii and A. australis), n = 100).

Early in the study, an investigation was made of the feasibility of using an emetic to collect stomach contents of G. vulgaris. The emetic used in the trials was antimony potassium tartrate (tartar emetic) which acts by local irritation of the stomach. Although this emetic has been used with success in larger species of fish, e.g. walleye, Stizostedium vitreum (Jernejcic, 1969), it proved unsatisfactory for use with G. vulgaris. The administration of the emetic to the stomach of G. vulgaris, via plastic tubing (internal diameter = 1 mm) attached to a syringe, was difficult under field conditions and the dosages required to produce complete emptying of the stomach normally resulted in the death of the fish. Therefore, this method of collection of stomach contents was abandoned in favour of the traditional method of killing the fish and removing the stomach. In practice, fish were anaesthetized before being

placed in preservative; the stomach was then removed and stored in 10% formalin. The contents of each individual stomach were examined in water in a petri dish under a low-power (x6.3 - x40) binocular microscope.

Samples were taken of the drift and bottom organisms in the River Glentui in order to aid the identification of food items found in the stomachs. Normally, food organisms were identified to genus, while in some instances, identification to species was possible. A list of the macro-fauna of the River Glentui is presented in section 1.(3) of Chapter II. The identification of the invertebrate fauna was aided by Wisely (1961, 1965), Marples (1962), Penniket (1964, unpublished), Pendergrast and Cowley (1966), Stout (1969), Winterbourn (1970) and C.S.I.R.O. (1970). The simuliids and chironomids were identified by Crosby (pers. comm.) and Winterbourn (pers. comm.) respectively.

(2) Enumeration of stomach contents

Hynes (1950) and Windell (1968) reviewed the methods used in the assessment of fish stomach contents and indicated the advantages and disadvantages of each method. In the present study, both the occurrence and the points methods were used. In the occurrence method, the number of stomachs in which each food item occurs is recorded and expressed as a percentage of the total number of stomachs examined in each sample. In the points method, proposed by Swynnerton and Worthington (1940) and later adopted with modifications by a number of workers (e.g. Frost, 1943; Van Someren, 1946; Hynes, 1950; Graham and Jones, 1962), each food item is allotted points depending upon abundance and size. The points allotted to each type of food item are then summed and expressed as a percentage of the total number of points allotted to all food items in all stomachs in the sample. In the present study, the allocation of points in all species examined was based on a standard allocation drawn up for G. vulgaris (see Table 27). The degree of stomach fullness was estimated visually using the criteria proposed by Ball (1961).

TABLE 27. Maximum points allotted to G. vulgaris stomachs of different degrees of fullness.

Total length (mm)	Maximum points allotted to stomachs in the following condition: half full	full	distended
30 - 60	4	8	16
61 - 90	6	12	24
> 90	8	16	32

As pointed out by Windell (loc. cit.), the occurrence method provides no information on the quantity of each food item consumed and does not take into account the accumulation of parts of organisms resistant to digestion. In the points method, which is essentially an approximate volumetric method, the subjective allocation of points by the investigator is the major limitation. Frost (1939), comparing the results obtained by the occurrence, dominance and numbers methods, indicated that all methods give essentially the same results, although the numbers method tends to overestimate the importance of small organisms. The results obtained by the occurrence and the points methods were compared, in the present investigation, by computing the product-moment correlation coefficient (Sokal and Rohlf, 1969), between the percentage points and the percentage occurrence of the same eight food items in different-sized samples of G. vulgaris stomachs (see Table 28). It may be seen from the high correlation coefficients that the results of the two methods were similar and that the similarity tended to increase with increasing sample size. Therefore, for large samples ($n > 50$), both methods of assessment were considered to be of equal merit in indicating the relative importance of various items in the diet. However, for small samples ($n < 50$), more reliance was placed on the results obtained by the points method, since, of the two methods used, it was considered to provide the more accurate estimate of the diet. However, in a number of instances, e.g. with the early instars of Diptera, although a particular food item was recorded by the occurrence method, it did not merit the allocation of a point and so was not recorded by the points method.

TABLE 28. Product-moment correlation coefficients (r) between the percent points and the percent occurrence of the same eight food items (viz. Archichauliodes diversus larvae; Coloburiscus humeralis larvae; Nesameletus sp. larvae; Deleatidium spp. larvae; Hydropsyche colonica larvae; Hydrobiosis sp. larvae; Pycnocentrodes sp. larvae; dipteran larvae, pupae and adults) in different-sized samples of G. vulgaris stomachs. (n = sample size; A = age group sample; L = length group sample (in mm); M = monthly sample; + = all G. vulgaris stomachs sampled between June 1970 and May 1971).

Sample	Type	n	r	95 % CL lower	95 % CL upper
annual	+	701	0.9243	0.6297	0.9865
0+	A	307	0.9395	0.6946	0.9893
50 - 59	L	213	0.9628	0.8025	0.9935
1+	A	177	0.9692	0.8342	0.9946
80 - 89	L	154	0.9534	0.7577	0.9918
60 - 69	L	147	0.9339	0.6704	0.9882
July	M	139	0.9906	0.9488	0.9984
70 - 79	L	120	0.9618	0.7978	0.9933
April	M	111	0.8127	0.2526	0.9648
2+	A	109	0.8611	0.3976	0.9745
90 - 99	L	89	0.9670	0.8232	0.9942
May, 1-2	M	69	0.6824	-0.0431	0.9367
March	M	64	0.9560	0.7702	0.9922
100 - 109	L	59	0.9134	0.5855	0.9844
November	M	51	0.9152	0.5927	0.9848
3+	A	45	0.8871	0.4865	0.9795
August	M	44	0.7385	0.0702	0.9492
June	M	30	0.9778	0.8780	0.9661
May, 29-30	M	25	0.7414	0.0766	0.9498
October	M	24	0.9843	0.9126	0.9973
>110	L	14	0.8536	0.3737	0.9730

(3) Analysis of data

The analysis of data was greatly facilitated by transferring all information to computer cards and using an IBM 360/44 computer to sort the data. A similar system was used by Corbet (1961).

The degree of similarity between the diets of pairs of samples (both intra- and interspecific), estimated by both the points and occurrence methods, was measured by means of the nonparametric Kendall rank correlation coefficient (Siegel, 1956; Sokal and Rohlf, 1969). Firstly, the food items in each sample were ranked in descending order of importance; in the event of a tie within a rank, the tied observations were given the average of the ranks they would have received if there had been no ties. The Kendall rank correlation coefficient, τ (tau), was then calculated, using the formula:

$$\tau = \frac{S}{\frac{1}{2}N(N-1)} \qquad (1)$$

where S is the observed sum of the +1 and -1 scores allocated by inspection of the relative position of each item in both ranks (see example below) and N is the number of items in a rank. For tied observations the formula is modified to:

$$\tau = \frac{S}{\sqrt{\frac{1}{2}N(N-1) - Ta}\sqrt{\frac{1}{2}N(N-1) - Tb}} \qquad (2)$$

where $Ta = \frac{1}{2} \sum t(t-1)$, where t is the number of tied observations in each group of ties in rank A, and $Tb = \frac{1}{2} \sum t(t-1)$, where t is the number of tied observations in each group of ties in rank B. To standardize all comparisons, the same 15 food categories were used in all computations of the coefficient. The choice of the categories was based on the 15 most common items (determined by both the points and occurrence methods) found in the stomachs of all fish species in the River Glentui (viz. G. vulgaris, P. breviceps, S. trutta, A. dieffenbachii and A. australis). The 15 categories chosen were:

1. Deleatidium spp. larvae
2. Nesameletus sp. larvae
3. Coloburiscus humeralis larvae

TABLE 29. Data used to calculate the Kendall rank correlation coefficient between the diet of age 0+ (sample A) and age 1+ (sample B) G. vulgaris, determined by the frequency of occurrence method. (L = larva, P = pupa, A = adult) (N = 15).

	Sample A		Sample B		Allocation of points	
	% occ.	rank	% occ.	rank	+	-
Deleatidium spp. L.	52.1	1	65.5	1	14	0
dipteran L, P, A.	19.9	2	17.6	2	13	0
Hydrobiosis sp. L.	9.4	3	13.0	5	10	2
Nesameletus sp. L.	6.2	4	17.5	3	11	0
Pycnocentrodes sp. L.	4.6	5	11.0	6	9	1
H. colonica L.	3.2	6	8.5	7	8	1
terrestrial arthropods	2.0	7	6.8	8	7	1
A. diversus L.	1.6	8.5	5.6	10	5	2
C. humeralis L.	1.6	8.5	14.1	4	6	0
other cased caddis L.	1.0	10	3.4	12	3	2
Olinga sp. L.	0.3	11.5	4.0	11	3	1
coleopteran L, P, A.	0.3	11.5	5.7	9	3	0
plecopteran L.	0	14	1.2	13	2	0
P. antipodarum	0	14	0	14.5	0	0
Vertebrata	0	14	0	14.5	0	0
					94	10

4. Archichauliodes diversus larvae
5. plecopteran larvae (Stenoperla, Zelandoperla, Aucklandobius spp.)
6. Hydrobiosis sp. larvae
7. Hydropsyche colonica larvae
8. Olinga sp. larvae
9. Pycnocentrodes sp. larvae
10. larvae of other cased Trichoptera (Helicopsyche, Hudsonema, Beraeoptera, Triplectides, Oxyethira spp.
11. dipteran larvae, pupae and adults
12. coleopteran larvae, pupae and adults
13. Potamopyrgus antipodarum
14. terrestrial arthropods
15. vertebrates

In the following example of the computation of the Kendall rank correlation coefficient, the degree of similarity between the diets of age 0+ G. vulgaris (Sample A) and age 1+ G. vulgaris (Sample B) is estimated. The data are derived from the frequency of occurrence method (see Table 29).

Firstly, the food items in sample A are ranked in order of decreasing importance (see Table 29). The value of S is then computed by taking each item in sample B in turn and allocating a score of +1 to each of the following items which is in natural order, and allocating a score of -1 to each of the following items which is not in natural order, e.g. the food item H. colonica is ranked 7 in sample B; eight of the items following H. colonica are in natural order with respect to 7, i.e. they are greater than 7, so that a score of +1 is allocated to each of these eight items; one item following H. colonica is not in natural order, viz. C. humeralis which is ranked 4, so that this item is allocated a score of -1. The +1 and -1 scores for all items in sample B are then summed, giving a value of 84 (i.e. 94 - 10) for S.

Since tied observations are present in the ranks, formula (2) must be used. In sample A, there are three sets of tied observations: two sets of two items (ranked at 8.5 and 11.5) and one set of three items (ranked at 14). In sample B, there is one set of tied observations,

consisting of two items ranked at 14.5. Thus Ta and Tb are computed:

$$Ta = \tfrac{1}{2}(2(2-1) + 2(2-1) + 3(3-1))$$
$$= 5$$

$$Tb = \tfrac{1}{2}(2(2-1))$$
$$= 1$$

Since N, the number of items in each rank, = 15, the Kendall rank correlation coefficient is:

$$\tau = \frac{84}{\sqrt{\tfrac{1}{2}\,15(15-1) - 5}\sqrt{\tfrac{1}{2}\,15(15-1) - 1}}$$
$$= 0.824$$

The significance of τ for sample sizes greater than 10 may be tested by using a normal approximation to test the null hypothesis that the true value of $\tau = 0$, using the formula given by Siegel (loc. cit.:221) and Sokal and Rohlf, (loc. cit.: 536):

$$z = \frac{\tau}{\sqrt{2(2N+5)/9N(N-1)}}$$

The significance of z may then be determined by reference to a table of areas of the normal curve.

For the above example,

$$z = \frac{0.824}{\sqrt{2(2(15)+5)/9(15)(15-1)}}$$
$$= 4.28$$

By referring to a table of areas of the normal curve, it may be seen that the probability of such a value of z arising by chance = 0.00001 (both tails). Thus, the null hypothesis is rejected and it is concluded that samples A and B are associated or, in other words, the diets of age 0+ and age 1+ G. vulgaris, determined by the occurrence method, are very similar.

Probability values greater than 0.05 were considered to indicate that the diets being compared were dissimilar. With reduced probabilities, the degree of similarity of the diets increased; from 0.05 to 0.01, the diets were considered to be similar and for probabilities less than 0.01, the diets were considered to be very similar. Thus,

FIGURE 29. Monthly and annual diet of G. vulgaris in the River Glentui from June 1970 to May 1971, assessed by the occurrence method. (Fish sample sizes: June (J) = 30, July (J) = 139, August (A) = 44, September (S) = 39, October (O) = 24, November (N) = 51, December (D) = 31, January (J) = 24, February (F) = 50, March (M) = 64, April (A) = 111, May 1-2 (M) = 69, May 29-30 (M') = 25, Total = 701.)

The key to the food organisms (numbered 1 - 20) is on the blue fold-out page (following page 101).

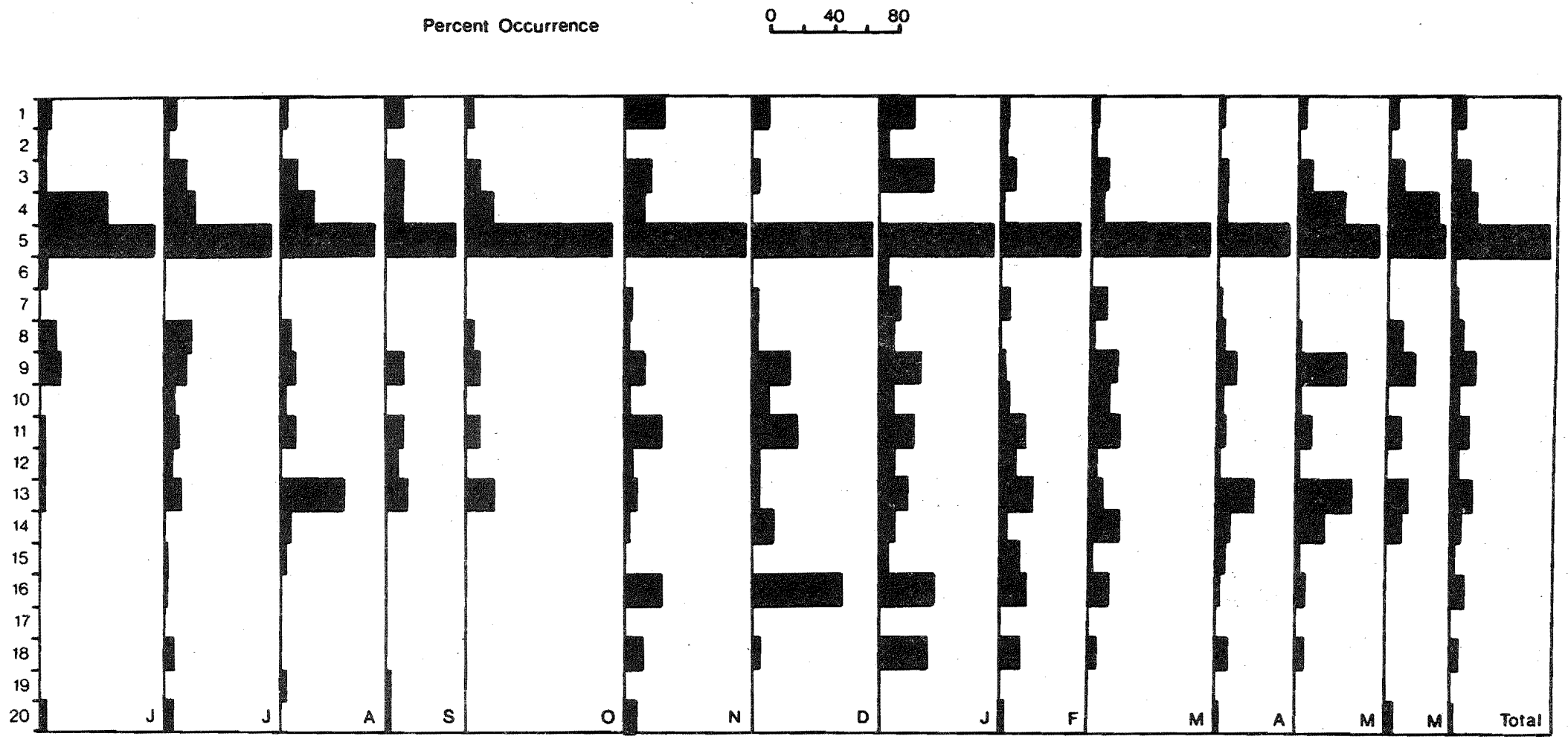
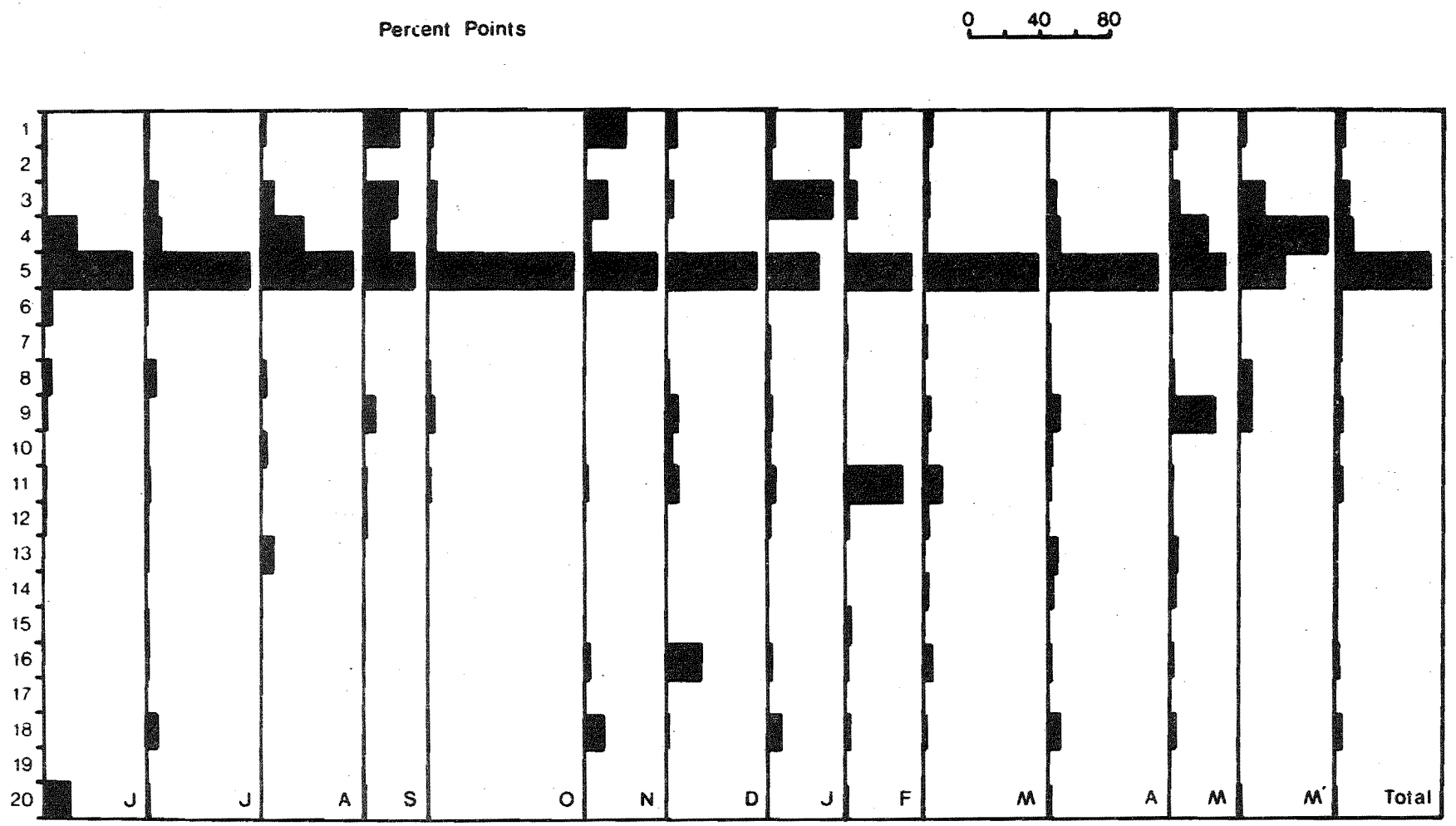

Percent Occurrence
0
40
80
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
J
J
A
S
O
N
D
J
F
M
A
M
M
Total

FIGURE 30. Monthly and annual diet of G. vulgaris in the River Glentui from June 1970 to May 1971, assessed by the points method. (Fish sample sizes are as in Fig. 29).

The key to the food organisms (numbered 1 - 20) is on the blue fold-out page (following page 101).


Percent Points
0
40
80
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
J
J
A
S
O
N
D
J
F
M
A
M
M'
Total

values of τ were used to indicate the degree of similarity of the diet of pairs of samples. Rogers (1968) used a similar rank correlation coefficient to compare the diets of threespine sticklebacks, Gasterosteus aculeatus, and the fry of sockeye salmon, Oncorhynchus nerka. A different technique was employed by Zaret and Rand (1971) who used the overlap measure of Morisita (1959), as modified by Horn (1966), to estimate the degree of overlap in the food of fish inhabiting a tropical stream.

As pointed out by Mann and Orr (1969), who used the numerical method of assessment of stomach contents, one of the difficulties in interpreting data from stomach analyses is that variation in the number of food organisms is often greater between the individuals from one sample, than between the mean values of two samples. From the results of an analysis of variance, they concluded that little importance should be attached to small differences between the mean numbers of organisms in different samples, particularly if the samples are small and the within-sample variances large. The same argument holds for other methods of assessment of stomach contents and must be borne in mind when interpreting results.

2. Diet of G. vulgaris

The monthly diet of G. vulgaris caught in riffle areas in the River Glentui, from June 1970 to May 1971, together with the total diet for this period, is presented in Figs. 29 (occurrence method) and 30 (points method).

Ephemeropteran larvae, particularly Deleatidium spp. and to a less extent C. humeralis and Nesameletus sp., were the most important food items in the diet. Zephlebia sp. and Oniscigaster sp. occurred infrequently. Adult Ephemeroptera were taken in summer and autumn; they were found in only 14 of the 701 stomachs examined, but constituted 4.4% of the total number of points (2,279) allotted to stomach contents during this period.

Both free-living and cased trichopteran larvae figured prominently in the diet. Of the free-living caddises, Hydrobiosis sp. (Family Rhyacophilidae) was the most common, although H. colonica was also taken quite regularly. Of the cased caddises, Pycnocentrodes sp., with

its small trumpet-shaped case made of small stones, was the most common. This was followed by Olinga sp., the larvae of which possess a horny, trumpet-shaped case. Other cased caddises were found infrequently: Pycnocentria sp. was found in 12 stomachs, Beraeoptera sp. in eight, whilst Helicopsyche sp., Hudsonema sp., Triplectides sp. and Oxyethira sp. were each found in one stomach. Adult Trichoptera were found in only two stomachs, one sampled in July and the other in November.

Larvae of the neuropteran A. diversus, although occurring in only 44 stomachs, constituted, on the basis of allocated points, 5.4% of the total diet.

Larvae of aquatic Diptera, particularly chironomids and simuliids, occurred quite regularly and were often present in large numbers. However, because of their small size, they accounted for less than 2% of the diet, on a points basis. The chironomid larvae included Maoridiamesa harrisi and species of Orthocladiinae, Tanytarsini and Anatopynia. Pupae of Anatopynia sp. were found in two stomachs, whilst adults of M. harrisi and Orthocladiinae were each found in one stomach. Larvae of Austrosimulium multicorne and Austrosimulium ungulatum were found in 41 stomachs, whilst one adult simuliid was found in a stomach sampled in November. Other aquatic dipterans found in the diet included pupae and adults of Tipulidae (found in five and two stomachs respectively) and larvae of Dixidae (found in seven stomachs).

Larvae and adults of Elmidae were found in approximately equal numbers and contributed substantially to the diet, particularly in the summer months. A larva of another aquatic coleopteran, belonging to the family Helodidae, was found in one stomach sampled in July.

Plecopteran larvae were found only on a few occasions: Stenoperla sp. was found in three stomachs, whilst Zelandoperla sp. and Aucklandobius sp. were each found in one stomach. An adult plecopteran was found in one stomach sampled in November.

The remains of one P. breviceps was found in one stomach taken in November. Galaxias vulgaris eggs were found in two fish; five eggs were found in the stomach of one male, 94 mm long, taken in August and one egg was found in the stomach of another male, 92 mm long,

taken in September. The number of eggs present in each stomach suggests that the eggs were stray eggs (see Chapter IV); larger numbers would be expected if the fish had been feeding on an egg mass.

Gordius pachydermus (Nematomorpha) was found in one stomach sampled in July.

Food of terrestrial origin included lumbricids and a wide variety of arthropods, consisting mainly of insects of the orders Hymenoptera, Coleoptera, Lepidoptera, Orthoptera and Diptera. Lumbricids were found in only five stomachs, taken in June and July, but, because of their large size, they constituted 2% of the total diet, on a points basis. Terrestrial arthropods were found in 96 stomachs, mainly in those sampled in the summer months, and formed a substantial part of the diet.

Plant material was present in only eight stomachs and consisted of seed cases, leaves and small pieces of twig and bark, all of terrestrial origin.

Thus, most of the diet was composed of organisms of aquatic origin. Material of terrestrial origin made up only 11.2% of the total diet, on a points basis, and, of this, 4.6% was due to adult Trichoptera, Ephemeroptera and Plecoptera which were derived ultimately from aquatic larvae.

Nikolsky (1963:284) recognized three types of food consumed by fish, on the basis of importance in the diet, viz. basic food, i.e. that which is normally eaten by the fish, comprising most of the stomach contents; secondary food, i.e. that which is frequently found in the stomach, but in smaller amounts and incidental food, i.e. that which is found only rarely in the stomach contents. In G. vulgaris the basic food consisted of the larvae of Deleatidium spp., C. humeralis and Nesameletus sp., which occurred in 83.1% of the stomachs examined and comprised 69.6% of the total diet, on a points basis. Secondary food, comprising 27.3% of the total diet, consisted of terrestrial arthropods, elmids and the larvae of Hydrobiosis sp., H. colonica, A. diversus, Olinga sp., Pycnocentrodes sp., chironomids and simuliids. The remaining items in the diet were regarded as incidental food.

Similarly, G. maculatus was found to have carnivorous feeding

habits and to take a wide variety of aquatic and terrestrial organisms, particularly chironomid larvae and pupae, Copepoda and Potamopyrgus (McDowall, 1968a). Hopkins (1971a) also found that the food of G. divergens included most of the common small invertebrates in the study stream, with the larvae of Deleatidium spp. and chironomids predominating.

TABLE 30. Kendall rank correlation coefficients for comparisons of the diet of G. vulgaris in winter (n = 210), spring (n = 113), summer (n = 104) and autumn (n = 239). Figures in parenthesis are values of z for testing the significance of τ. The top right portion of the table contains the results of comparisons based on the occurrence method; the bottom left portion of the table contains the results of comparisons based on the points method.

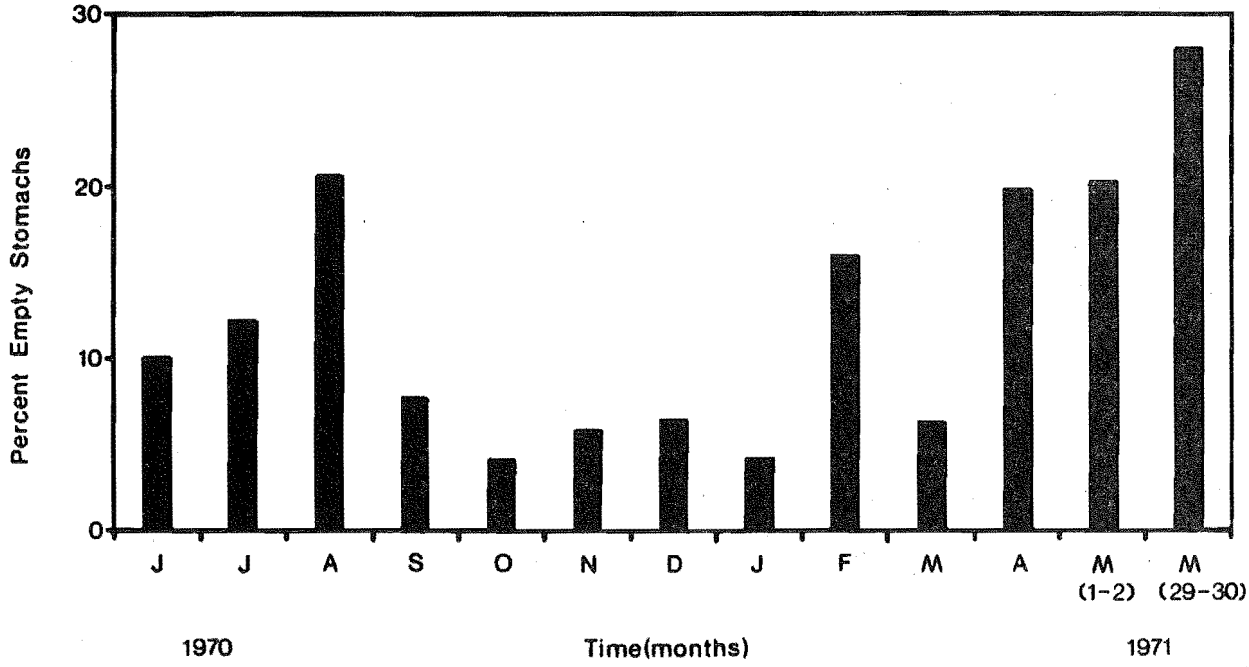
	Winter	Spring	Summer	Autumn
Winter	-	0.5196	0.3862	0.6699
		(2.7001)**	(2.0068)*	(3.4809)***
Spring	0.5686	-	0.5174	0.6108
	(2.9547)**		(2.6886)**	(3.1740)**
Summer	0.3565	0.4357	-	0.6931
	(1.8522)	(2.2638)**		(3.6015)***
Autumn	0.5686	0.4902	0.4951	-
	(2.9547)**	(2.5471)*	(2.5725)*	

* probability 0.05 - 0.01
** probability 0.01 - 0.001
*** probability < 0.001

(1) Seasonal variation in the diet and intensity of feeding

To examine seasonal differences in the diet, the monthly samples were divided into four groups representing winter (June, July, August), spring (September, October, November), summer (December, January, February) and autumn (March, April, May). The Kendall rank correlation coefficients between pairs of these samples (see Table 30) indicated that

FIGURE 31. Percent occurrence of empty stomachs in samples of G. vulgaris taken between June 1970 and May 1971. (Sample sizes are as in Fig. 29).


30
20
10
0
Percent Empty Stomachs
J
J
A
S
O
N
D
J
F
M
A
M
(1-2)
M
(29-30)
1970
Time(months)
1971

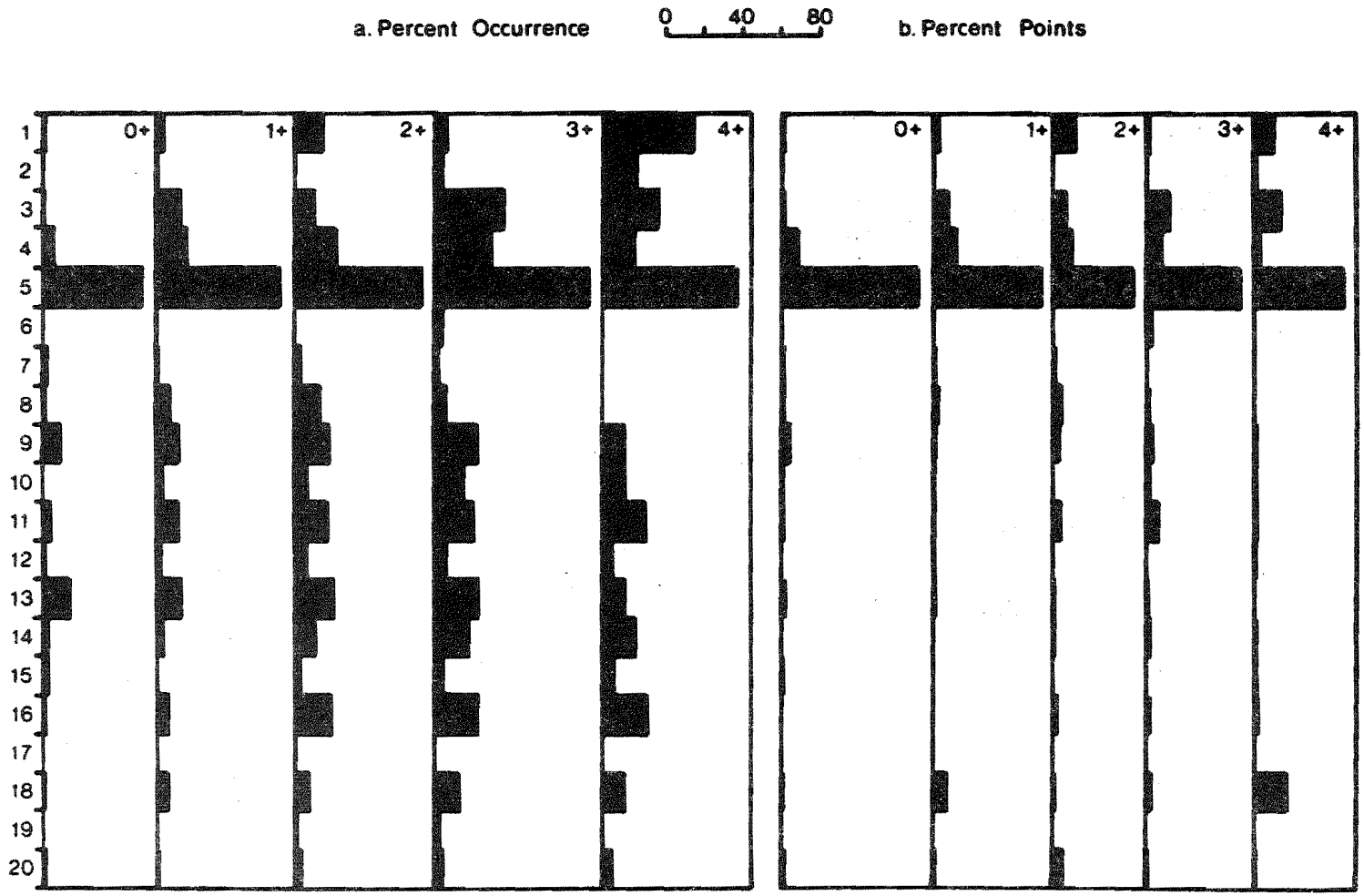
the degree of similarity in the diets was greatest between adjacent seasons. The greatest difference was that between summer and winter. This was mainly caused by an increase in the number of Elmidae and terrestrial arthropods, and to a less extent Pycnocentrodes sp. larvae, and a reduction in the number of Nesameletus sp. larvae taken during the summer months (see Figs 29 and 30). Such seasonal variation has been found in the diet of a number of species (see, e.g. Webster, 1954; Nilsson, 1955, 1958; Ball, 1961; Northcote and Lorz, 1966; Larsen, 1967; Hellawell, 1971a,b; Hunt and Jones, 1972) and has usually been correlated with the relative availability of the dietary items. In the present study, no information was obtained on the relative availability of the benthic and drift fauna at different times of the year, but terrestrial arthropods were plentiful only in the summer months.

The proportion of empty stomachs in samples of G. vulgaris taken between June 1970 and May 1971 is presented in Fig. 31; in all samples fish were collected between 0900 and 1700 hours. It may be seen that the proportion of empty stomachs was highest in samples taken during the autumn and winter months, and lowest in samples taken during spring.

Metabolic requirements are reduced at low temperatures (see Chapter III) so that in temperate regions, assuming a constant food supply, food consumption may be expected to be less in winter than in summer. Furthermore, Keast (1968) found that fish consumed a much smaller range of prey items at low temperatures than at higher ones. However, the larger proportion of empty G. vulgaris stomachs found in autumn than in winter (17.5% and 13.6% respectively) and in summer than in spring (10.5% and 6.1% respectively) indicate that other factors, perhaps changing photoperiod (Gross, Roelofs and Fromm, 1965; Johnson, 1966), may also play an important role. The relatively large proportion of empty stomachs found in late winter (August) may be associated with spawning. At this time of the year there is a reversal of the normal diel activity cycle (see later), so that during this period G. vulgaris is active mainly during daylight. Since G. vulgaris normally feeds at night (see later), it would be expected that a shift to diurnal activity would affect food consumption. Trent and Hassler (1966) found that striped bass, Roccus saxatilis, ceased feeding for a brief period

FIGURE 32. Diet of G. vulgaris in different age groups, assessed by (a) the occurrence method and (b) the points method. Included are those fish sampled in riffle areas from June 1970 to May 1971; recently-hatched fish sampled in quiet stretches of the River are not included. (Sample sizes: age 0+ = 307, age 1+ = 177, age 2+ = 109, age 3+ = 45, age 4+ = 17).

The key to the food organisms (numbered 1 - 20) is on the blue fold-out page (following page 101).


a. Percent Occurrence
0
40
80
b. Percent Points
0+
1+
2+
3+
4+
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20

just before and during the spawning period.

Within the normal temperature range of a species, the rate of gastric digestion is higher at high temperatures than at low temperatures (see, e.g. Sokolov and Chvaliova, 1936; Reimers, 1957; Molnar and Tolg, 1962a,b; Tyler, 1970; Elliott, 1972), so that in the summer months, food is generally digested more quickly than in the winter months. If the same amount of food was consumed throughout the year, this would tend to increase the number of empty stomachs found in the summer months.

The rate of gastric emptying and feeding may also be affected by the quantity of food consumed. Windell (1967), Kitchell and Windell (1968) and Tylor (1970) demonstrated that an increased quantity of food in the stomach resulted in an increase in the rate of gastric emptying.

Thus, assuming that the feeding cycle of G. vulgaris is constant throughout the year (evidence presented later suggests that this is so, with the exception of the immediate pre-spawning period), the low proportion of empty stomachs in the spring and summer months may be regarded as being indicative of an increase in food consumption during these months. Such an increase has been reported for a number of fish inhabiting temperate waters (see e.g. Hellawell, 1971b).

(2) The relationship between diet and age

The diets of fish aged from 0+ to 4+ are presented in Fig. 32. To clarify comparisons, only those fish caught in the same type of habitat, viz. riffle areas, and consequently exposed to the same type of food organisms, are included in this analysis; recently-hatched fish caught in the quiet stretches of the River are not included. The most salient feature of Fig. 32 is the increase in importance of large food items, such as Archichauliodes diversus larvae (which reach up to 36 mm in length), Coloburiscus humeralis larvae and terrestrial arthropods, with increasing age. Aquatic Coleoptera (mostly Elmidae) were also taken more frequently by the older age groups. These changes in the diet with increasing age are indicated by the Kendall rank correlation coefficients for comparisons of the diet of the different age groups (see Table 31); the coefficients tend to decrease with increasing age gap between samples. However, the diet did not change significantly with increasing age (probability in all comparisons <0.05).

FIGURE 33. Diet of G. vulgaris in different total length groups (in mm), assessed by the occurrence method. (Sample sizes: 30 – 39 mm length group = 17, 40 – 49 = 51, 50 – 59 = 213, 60 – 69 = 147, 70 – 79 = 120, 80 – 89 = 154, 90 – 99 = 89, 100 – 109 = 59, >110 = 14).

The key to the food organisms (numbered 1 – 20) is on the blue fold-out page (following page 101).

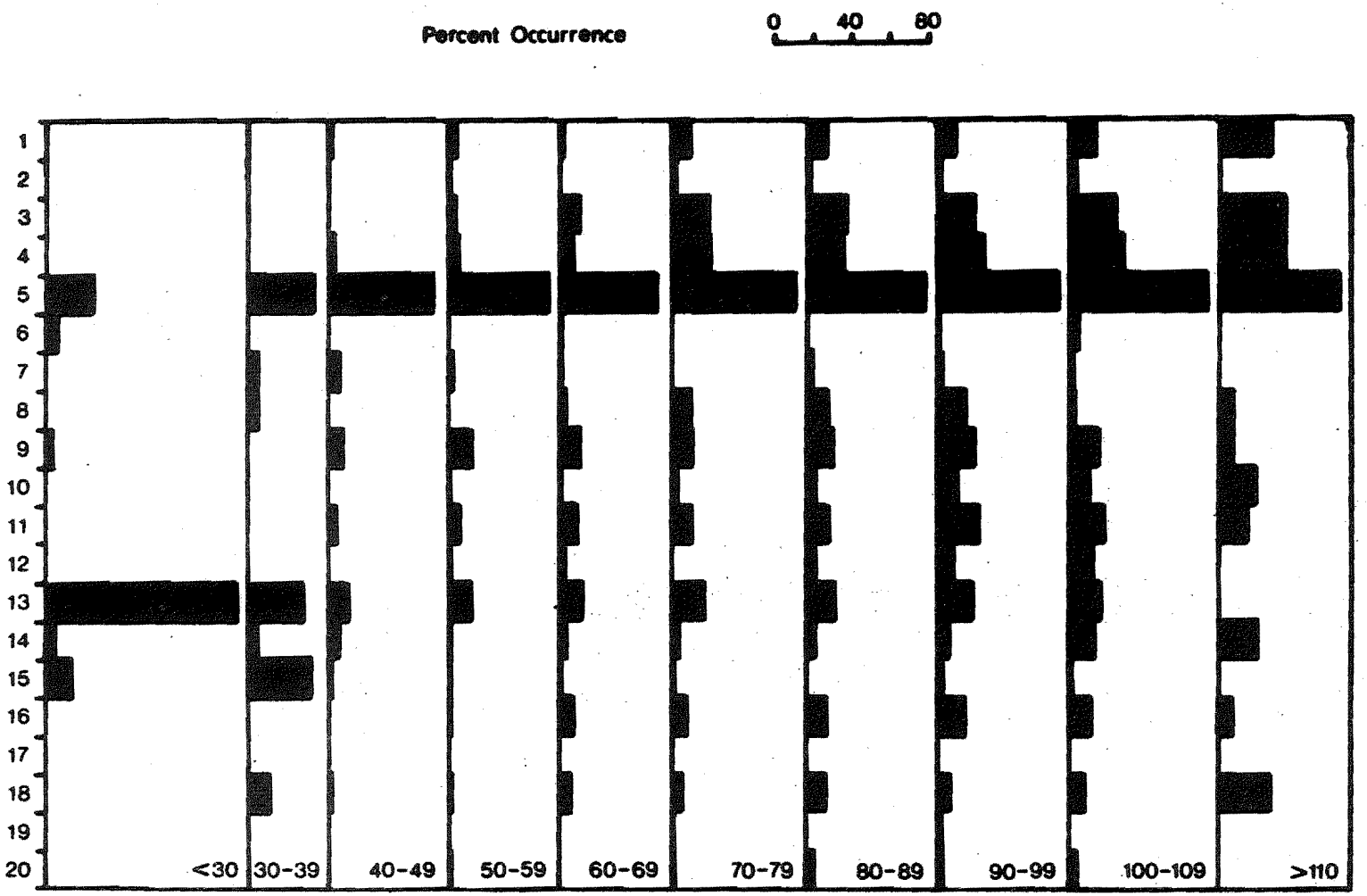

Percent Occurrence
0
40
80
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
<30
30-39
40-49
50-59
60-69
70-79
80-89
90-99
100-109
>110

FIGURE 84. Diet of G. vulgaris in different total length groups (in mm), assessed by the points method. (Sample sizes are as in Fig. 83).

The key to the food organisms (numbered 1 - 20) is on the blue fold-out page (following page 101).

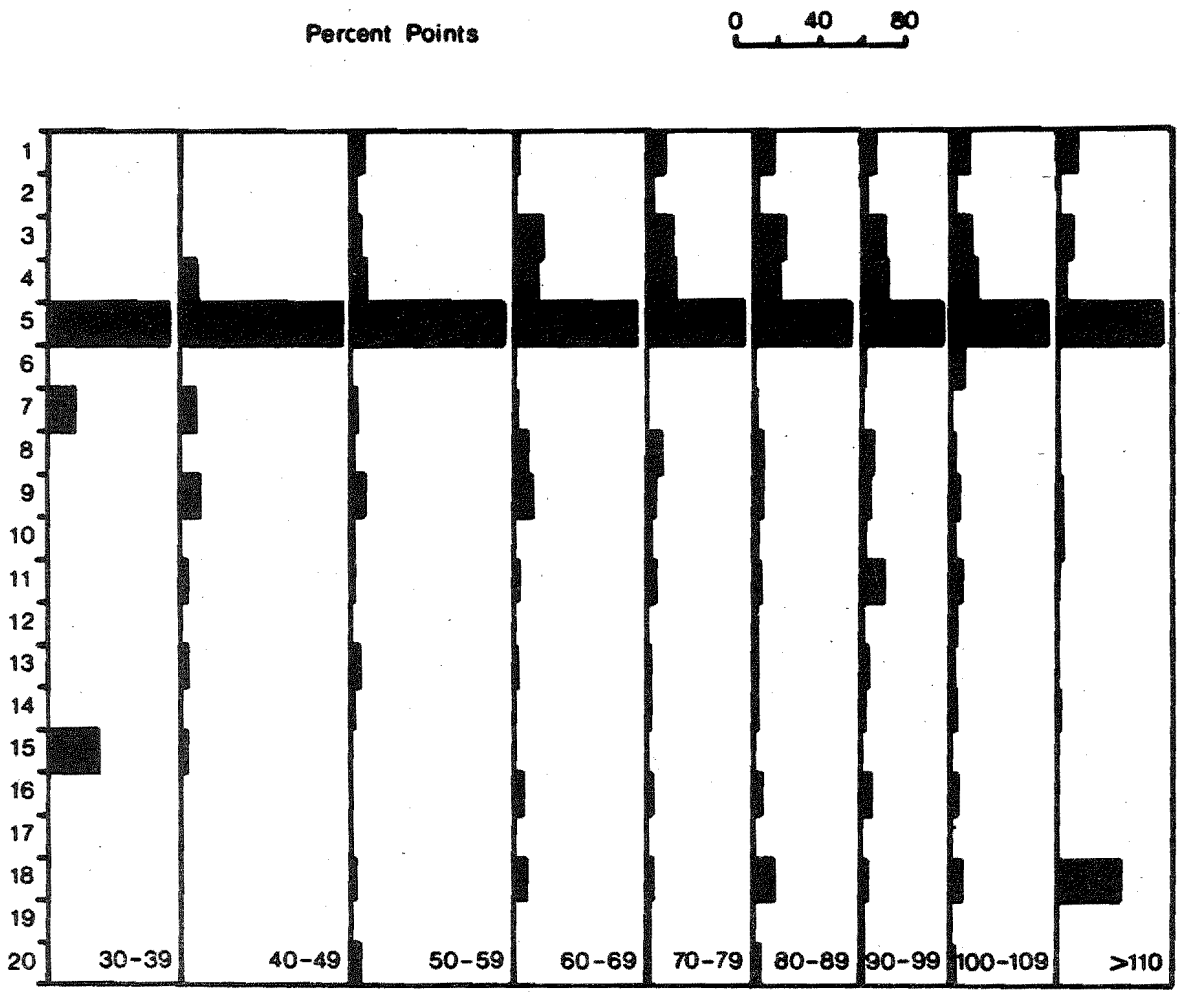

Percent Points
0
40
80
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
30-39
40-49
50-59
60-69
70-79
80-89
90-99
100-109
>110

TABLE 31. Kendall rank correlation coefficients for comparisons of the diet of G. vulgaris in different age groups. Figures in parenthesis are values of z for testing the significance of τ. The top right portion of the table contains the results of comparisons based on the occurrence method; the bottom left portion of the table contains the results of comparisons based on the points method.

	0+	1+	2+	3+	4+
0+	-	0.8237	0.7452	0.6269	0.4772
		(4.2800)***	(3.8724)***	(3.2573)**	(2.4797)*
1+	0.6809	-	0.7500	0.8078	0.5874
	(3.5381)***		(4.2800)***	(4.2081)***	(3.0523)**
2+	0.6878	0.6957	-	0.7513	0.6073
	(3.5736)***	(3.1648)**		(3.9039)***	(3.1558)**
3+	0.6740	0.5854	0.5631	-	0.6971
	(3.5024)***	(3.0417)**	(2.9261)**		(3.6223)***
4+	0.4376	0.5972	0.4953	0.6001	-
	(2.2738)*	(3.1031)**	(2.5735)**	(3.1183)**	

* probability 0.05 - 0.01
** probability 0.01 - 0.001
*** probability < 0.001

(3) The relationship between diet and fish size

This analysis includes all stomachs sampled from June 1970 to May 1971 (n = 761) and a further 163 stomachs sampled in November 1971. Fish were divided into 10mm length-groups; all fish smaller than 30 mm were included in one group and all fish larger than 110 mm were included in one group. The diet of each length-group is presented in Figs. 33 (occurrence method) and 34 (points method). Because of the small size of the stomachs, the occurrence method only was used to assess the diet of fish less than 30 mm in length.

It may be seen, as with increasing age, that there is an increase in the importance of the larger food items with an increase in fish size. There was also an increase in the variety of food items with increasing

TABLE 32. Kendall rank correlation coefficients for comparisons of the diet of G. vulgaris in different total length groups (in mm). Figures in parenthesis are values of z for testing the significance of τ. The top right portion of the table contains the results of comparisons based on the occurrence method; the bottom left portion of the table contains the results of comparisons based on the points method. (The points method was not used to assess the stomach contents of fish less than 30 mm in length).

	30 – 39	40 – 49	50 – 59	60 – 69	70 – 79	80 – 89	90 – 99	100 – 109	>110
< 30	1.0870 (5.6481)***	0.7951 (4.1318)***	0.8562 (4.4488)***	0.7488 (3.8912)***	0.8678 (4.5091)***	0.8362 (4.3452)***	0.6909 (3.5899)***	0.8562 (4.4488)***	0.4955 (2.5746)*
30 – 39	–	0.8655 (4.4972)***	0.7664 (3.9824)***	0.7177 (3.7291)***	0.7107 (3.6927)***	0.7842 (4.0746)***	0.4438 (2.3059)*	0.6441 (3.3470)***	0.6418 (3.3349)***
40 – 49	1.1577 (6.0154)***	–	0.8988 (4.6705)***	0.7239 (3.7612)***	0.8078 (4.1975)***	0.7775 (4.0398)***	0.6341 (3.2948)***	0.7546 (3.9210)***	0.5955 (3.0943)**
50 – 59	0.9593 (4.9844)***	0.8782 (4.5635)***	–	0.8138 (4.2285)***	0.8447 (4.3890)***	0.8586 (4.4611)***	0.7343 (3.8156)***	0.7220 (3.7514)***	0.5691 (2.9573)**
60 – 69	0.3155 (1.6393)	0.4284 (2.2260)*	0.6633 (3.4466)***	–	0.7549 (3.9228)***	0.8276 (4.3003)***	0.6440 (3.3462)***	0.7488 (3.3908)***	0.5132 (2.6664)**
70 – 79	0.1753 (0.9107)	0.5250 (2.7282)**	0.6769 (3.5173)***	0.7945 (4.1283)***	–	0.8781 (4.5625)***	0.7536 (3.9160)***	0.8000 (4.1570)***	0.6301 (3.2741)**
80 – 89	0.1727 (0.8975)	0.3291 (1.7103)	0.6472 (3.3627)***	0.8033 (4.1740)***	0.7415 (3.8532)***	–	0.7185 (3.7333)***	0.7647 (3.9735)***	0.6128 (3.1840)**
90 – 99	0.2367 (1.2298)	0.5088 (2.6439)**	0.6303 (3.2751)***	0.6641 (3.4509)***	0.8334 (4.3303)***	0.6860 (3.5646)***	–	0.7185 (3.7333)***	0.5462 (2.8380)**
100 – 109	0.2709 (1.4075)	0.4626 (2.4030)*	0.7173 (3.7273)***	0.6500 (3.3777)***	0.7228 (3.7556)***	0.7220 (3.7518)***	0.6961 (3.6171)***	–	0.5923 (3.0774)**
>110	0.2504 (1.3012)	0.2961 (1.5386)	0.7092 (3.6853)***	0.6379 (3.3144)***	0.6121 (3.1804)**	0.7770 (4.0372)***	0.5239 (2.7223)**	0.6432 (3.3421)***	–

* probability 0.05 – 0.01
** probability 0.01 – 0.001
*** probability < 0.001

fish size. Recently-hatched fish fed on only six food items, the larvae of Orthocladiinae predominating. Simuliid and tipulid larvae were also eaten, whilst Zephlebia sp. was more important, on the basis of frequency of occurrence, in this group than in any group of larger fish. Thus, dipteran larvae formed the basic food of fish less than 30 mm in length, with ephemeropteran and free-living trichopteran larvae being secondary foods. The change from a mainly dipteran diet to one of Ephemeroptera, particularly Deleatidium spp., occurred when fish reached about 40 mm in length. This coincides with the length at which fish normally leave the quiet stretches of the River and move into a riffle habitat.

The Kendall rank correlation coefficients between the diet of each length-group are presented in Table 32. It may be seen that, by the occurrence method, the diets of all length groups were similar. However, on the points method, the diets of the smaller fish (< 49 mm) were found to be significantly different from the diets of fish in the larger size groups.

A change in diet with an increase in size, with larger fish eating larger organisms, has been reported by a number of workers, (e.g. Ricker, 1930; Allen, 1938; Nilsson, 1955, 1958; Keast, 1966; Larsen, 1967; Munro, 1967; Hynes, 1970a:369). As pointed out by Thomas (1962), the gape of a fish determines to some extent the animals on which it feeds. However, as shown experimentally by Hartman (1958), although mouth size imposes a limit on the size of food eaten, the structure and behaviour of the food organisms may affect the size of the minimum gape required to feed on certain prey species. Selection by the fish may also be important (Allen, 1960); this may occur actively (see Allen, 1941) or passively and may be affected by the distribution of the prey organisms (Ivlev, 1946). Active selection may depend on experience, whereas passive selection depends on the natural habit of the species (Maitland, 1965). The natural habit of G. vulgaris changes at the end of the juvenile phase, when fish leave the quiet stretches of the River and become riffle-dwellers. In the riffle areas they have access to a more diverse fauna, including the larvae of Coloburiscus humeralis, Deleatidium spp., Archichauliodes

TABLE 33 Kendall rank correlation coefficients (τ) for comparisons of the diet of male and female G. vulgaris in (a) total length groups, (b) age groups and (c) season groups. Comparisons are made on the results obtained by both the occurrence and points methods.

	Sample size		% occurrence		% points	
	Male	Female	τ	z	τ	z
(a) TL groups						
30 - 49	32	34	0.7512	3.9032***	0.8328	4.3274***
50 - 59	100	109	0.9160	4.7956***	0.9281	4.8225***
60 - 69	69	78	0.8822	4.5838***	0.8169	4.2449***
70 - 79	66	54	0.8266	4.2950***	0.6432	3.3433***
80 - 89	61	93	0.8266	4.2950***	0.7898	4.1471***
90 - 99	41	48	0.7500	3.8973***	0.6139	3.1899**
>100	21	52	0.7248	3.7663***	0.6921	3.5960***
(b) Age groups						
0+	148	154	0.8528	4.4314***	0.8654	4.4967***
1+	81	96	0.7800	4.0530***	0.7326	3.8066***
2+	47	62	0.7762	4.0333***	0.7193	3.7375***
3+	21	24	0.9796	5.0901***	0.7803	4.0547***
4+	6	11	0.7344	3.8154***	0.5569	2.8935**
(c) Season groups						
Winter	106	104	0.8715	4.5276***	0.7863	4.0858***
Spring	48	65	0.6114	3.1768**	0.4977	2.8589**
Summer	47	57	0.8103	4.2103***	0.6563	3.4102**
Autumn	89	150	0.8283	4.3041***	0.6032	3.1344**

** probability 0.01 - 0.001
*** probability <0.001

diversus, Hydropsyche colonica, Hydrobiosis sp., Olinga sp., Pycnocentrodes sp. and simuliids, all of which are more common in riffle areas than in the more quiet parts of streams (Pendergrast and Cowley, 1966; McLay, 1968; Fowles, 1972 unpublished).

Percival (1932) proposed a scheme for the "food relations in inland waters of New Zealand". He suggested that juvenile trout, Galaxias and Gobiomorphus feed essentially on chironomids and Deleatidium sp., whereas the adult fish diversify to feed also on most of the other invertebrates present. This is basically the situation in G. vulgaris in the River Glentui, with the change from juvenile to adult diet corresponding with a change in habitat. Similarly, Hopkins (1971a) found that the early juvenile stages of G. divergens fed on chironomid larvae almost exclusively, but after attaining a length of about 35 mm they ate mainly Deleatidium spp. larvae. As pointed out by McDowall (1968a), this change is not applicable to G. maculatus, in which no diversification in food type occurs between the fish which have just migrated into freshwater and the adult fish.

(4) The diets of male and female G. vulgaris

Kendall rank correlation coefficients for comparisons of the diet of males and females in 10 mm length-groups, age-groups and season-groups are presented in Table 33. It may be seen that in all instances the diets of both sexes are very similar. However, for spring, τ is much lower than for the other seasons, on both the occurrence and points assessments. This may be the result of sexual differences in the feeding pattern during and after the spawning period, resulting from the differential attachment to the nest site of males and females (see Chapter IV). Also, τ for comparison of the diets of age 4+ males and females is relatively low, particularly on the points assessment. This may be explained, at least in part, by the difference in size of age 4+ males and females (see Table 3), females being more than 10 mm longer than males. The effect of size differences on the diet has been pointed out in the previous section.

3. Diel Periodicity in the Feeding of G. vulgaris

Benzie (1961, unpublished) suggested that G. vulgaris is nocturnal. Macfarlane (pers. comm. in Benzie, 1961 unpublished) reported that galaxiids (probably G. vulgaris or G. paucispondylus) were active

FIGURE 35. Apparatus used to measure the spontaneous locomotory activity of fish, (see text of section 3.(1) for explanation).

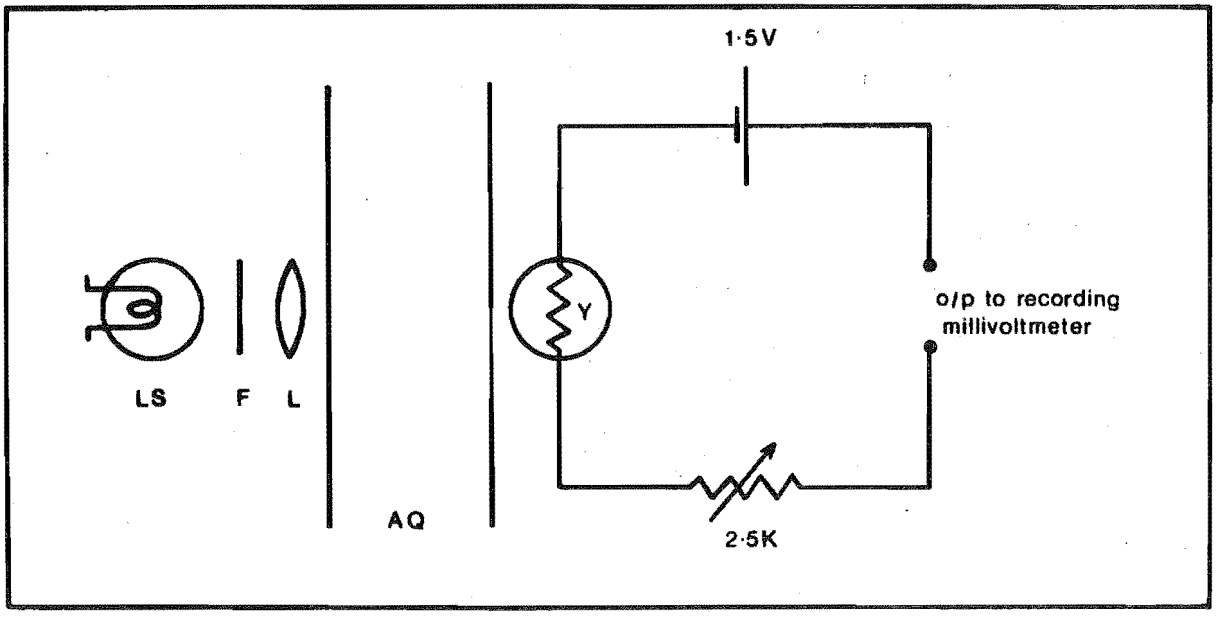
Key to letters:

LS = light source.

F = red filter

L = lens.

AQ = aquarium.


1·5V
LS
F
L
AQ
Y
o/p to recording
millivoltmeter
2·5K

in the Cass River at night. These observations were confirmed in the present study by observations made on G. vulgaris in laboratory aquaria and a stream tank throughout 24-hour periods. Observations were made through one-way glass set in a wooden screen, so that movements made by the investigator did not disturb the fish.

During the day, G. vulgaris remained beneath boulders on the substrate, only occasionally venturing into open water. However, at dusk there was an increase in activity: fish were found to spend more time in open water, often swimming just above the substrate. When at rest, they remained on the surface of the gravel and did not hide beneath boulders. This open-water behaviour was maintained throughout the hours of darkness. At sunrise, activity gradually decreased.

In general, unstarved fish were found to feed only at night. When they were feeding, food (ephemeropteran larvae and tubificids) was taken at the surface of the water, in mid-water and off the bottom. During the day, the presence of food did not normally stimulate feeding. However, with fish starved for 16 days, activity was less predictable and food was taken at all times, both during the day and at night.

Thus, activity and feeding were found to be correlated, the latter being the consequence of the former. Periods of locomotory activity were considered, primarily, to represent periods of food seeking. To obtain information on the diel periodicity of feeding throughout the year, the spontaneous locomotory activity of G. vulgaris was recorded quantitatively in a laboratory aquarium.

(1) Measurement of the spontaneous locomotory activity of G. vulgaris

A number of techniques have been used to measure the spontaneous locomotory activity of fish under laboratory conditions, (see Spencer, 1929a; Chaston, 1968b; Andreasson, 1969; Byrne, 1971; Schuyf and Groot, 1971). The experimental set-up used in the present study is shown in Fig. 35. Fish were held in a still-water aquarium (60 x 30 x 30 cm) with a substrate of gravel and boulders and a water depth of 4 cm. A beam of red light was focussed across the width of the aquarium onto a light-dependent resistor (L.D.R.). The variable resistance in the circuit was then adjusted to give zero deflection of the pen of a continuous

FIGURE 36. Spontaneous locomotory activity of individual G. vulgaris at different times of the year. Each histogram represents the mean values of the first three days after acclimatization in the apparatus, (see text of section 3. for explanation). Time between sunset and sunrise is indicated by a horizontal bar.

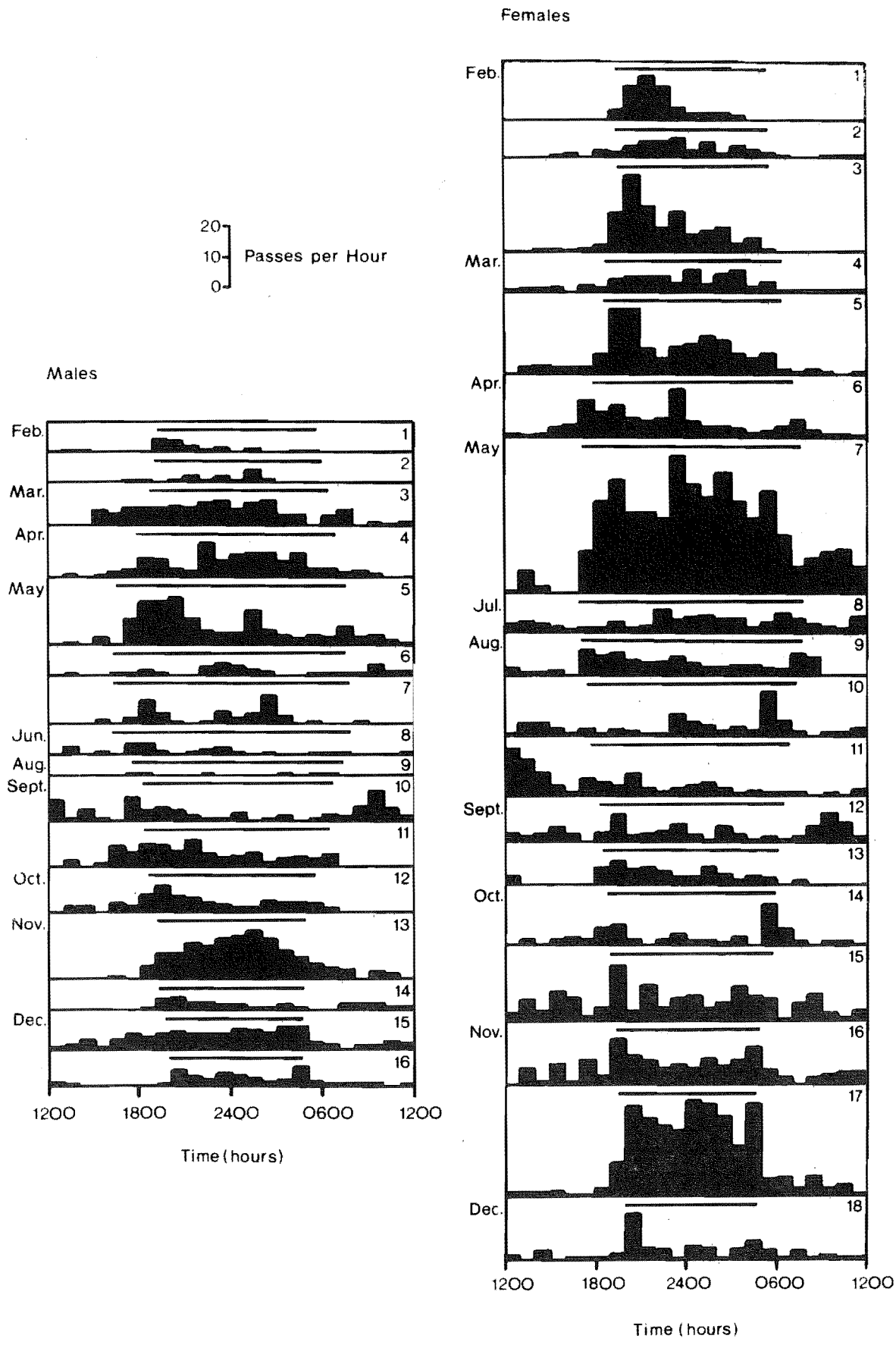

Females
Feb.
Mar.
Apr.
May
Jul.
Aug.
Sept.
Oct.
Nov.
Dec.
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
1200
1800
2400
0600
1200
Time (hours)
20
10
0
Passes per Hour
Males
Feb.
Mar.
Apr.
May
Jun.
Aug.
Sept.
Oct.
Nov.
Dec.
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
1200
1800
2400
0600
1200
Time (hours)

TABLE 34. Details of G. vulgaris used to measure spontaneous locomotory activity. Diel activity ratio = number of passes through beam per hour during night/number of passes through beam per hour during day (see text for further explanation). The reference numbers (No.) correspond to those used in Fig. 36.

Males					Females				
No.	Date	TL (mm)	age	diel activity ratio	No.	Date	TL (mm)	age	diel activity ratio
1	Feb., 9–14/72	79	1+	3.8	1	Feb., 4–8/72	98	2+	33.9
2	Feb., 19–22/72	99	2+	27.0	2	Feb., 15–18/72	109	3+	7.3
3	March,6–9/72	80	1+	2.7	3	Feb., 23–28/72	86	2+	9.6
4	April,19–21/71	87	1+*	5.7	4	March, 10–13/71	76	1+	5.1
5	May,4–6/71	85	1+	4.5	5	March, 14–17/72	77	1+	6.8
6	May,12–16/71	73	1+	1.7	6	March–Apr.,27–2/71	90	2+	1.8
7	May,28–31/71	64	0+	13.0	7	May, 8–11/71	85	2+	4.4
8	June, 8–12/71	75	1+	6.5	8	July, 19–24/71	85	1+	1.4
9	Aug., 15–19/71	104	3+	0.6	9	Aug., 6–10/71	96	3+	2.2
10	Sept., 19–22/71	74	0+	0.4	10	Aug., 11–14/71	59	0+	1.5
11	Sept., 25–29/71	87	2+	2.5	11	Aug.–Sept., 29–1/71	88	1+	0.6
12	Oct., 9–13/71	82	1+	3.0	12	Sept., 13–16/71	100	2+	0.9
13	Nov., 1–4/70	73	1+	6.4	13	Sept.–Oct., 30–3/71	107	2+	6.4
14	Nov., 14–18/70	66	1+	3.0	14	Oct., 18–21/70	79	1+*	1.6
15	Nov.–Dec., 27–1/70	59	1+	2.5	15	Oct., 23–27/70	95	3+*	1.9
16	Dec., 24–31/70	73	2+	6.9	16	Nov., 5–9/70	54	1+	2.2
					17	Nov., 19–22/70	84	2+	9.7
					18	Dec., 18–23/70	59	1+	3.7

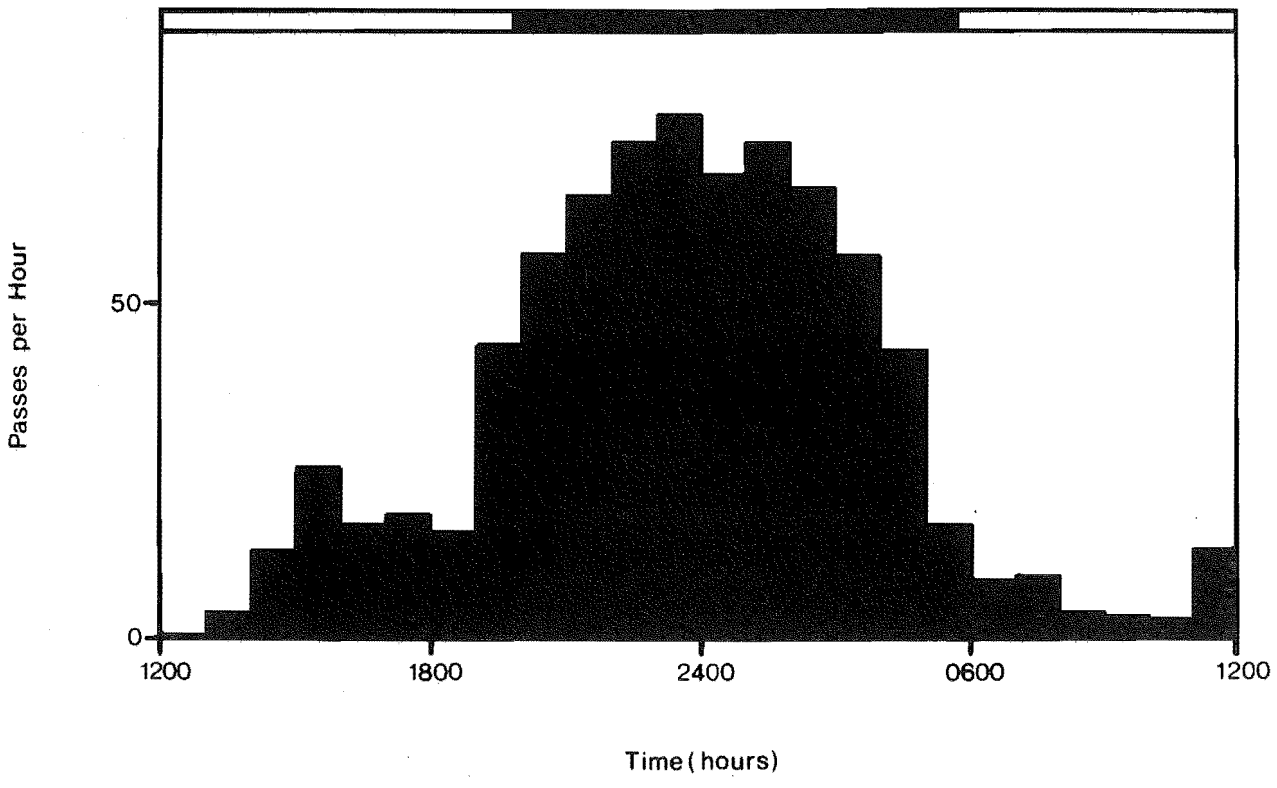
* these fish were aged by means of length frequency analysis; all other fish were aged from otoliths

recording millivoltmeter. When the beam was interrupted, by a fish swimming through it, the resistance of the L.D.R. increased and caused a deflection of the pen on the recording chart. Thus, the locomotory activity of fish was recorded. The L.D.R. was housed in a tube 10 cm long in order to prevent changes in resistance caused by different ambient light conditions, thereby ensuring that only the experimental light beam affected the resistance of the L.D.R. Red light, to which fish are relatively insensitive (Wald, 1940, but see Munz, 1971), was produced by placing a red filter (Kodak Wratten filter No. 25) in front of the light source. Fish did not appear to react in any way to the presence of the light beam. In the present investigation, only one beam was used, at a height of 2 cm above the substrate. For fish dependent on deeper water, a battery of separate beams and L.D.R. circuits may be used to cover the whole depth of the water. Before each experiment, the water in the aquarium was renewed and, to avoid any intraspecific reactions, single fish were used in each trial. Fish caught in the River Glentui were placed in the activity aquarium later the same day and were allowed 24 hours to acclimatize to the experimental conditions. Recordings were made for three to eight consecutive days (mean = 4.7 days) after the period of acclimatization, but, to standardize all comparisons, only the recordings for the first three days were used. No food was given to the fish once they had been taken from the River. The apparatus was completely surrounded by a screen to prevent outside disturbance and was situated in a position where it was subject to natural night-day conditions. Water temperature in the aquarium ranged from 12° to 21.5° C throughout the series of experiments.

(2) Results and discussion

The spontaneous locomotory activity of individual *G. vulgaris* at different times of the year is shown in Fig. 36: details of the fish used in each trial, together with its diel activity ratio, are presented in Table 34. The diel activity ratio is here defined as the number of passes through the beam per hour during night divided by the number of passes through the beam per hour during day, where night is defined as the period between sunset and sunrise, and day is the period between sunrise and sunset. All fish were taken from riffle areas in the River Glentui,

FIGURE 37. Spontaneous locomotory activity of a juvenile G. vulgaris (TL = 29 mm) measured between 28-1-71 and 31-1-71. The histogram represents the mean values of the first three days after acclimatization in the apparatus, (see text of section 3. for explanation). Time between sunset and sunrise is indicated by the shaded horizontal bar.


Passes per Hour
50
0
1200
1800
2400
0600
1200
Time (hours)

though fish of varying age and total length were used.

It may be seen that, normally, G. vulgaris is mainly nocturnal. This is interpreted as indicating that it feeds mainly at night. Since different individuals were used in each trial, no information was obtained on seasonal variation in spontaneous locomotory activity. Such variation that did occur probably reflected individual variation rather than seasonal variation. However, irrespective of the level of activity, the diel activity ratio was greater than 1 for most of the year. In August and September, diel activity ratios of less than 1 were reported for both males and females, indicating predominantly diurnal activity. This reversal of the normal pattern occurred during the spawning season. Indeed, the low recorded activity of one male (No. 9 in Fig. 36 and Table 34) was the result of nest-making in the gravel beneath one of the large boulders in the aquarium: its open-water activity was thereby reduced. Whether the reversal of the diel activity pattern is indicative of a change in feeding behaviour or an indication of spawning activity (and its associated movements within the River), or both, is uncertain. However, the large number of empty stomachs found in G. vulgaris sampled during the spawning period (see Fig. 31) indicates that feeding intensity is reduced at this time of the year. This suggests that the diurnal activity is associated with reproduction and that the reduced feeding intensity is associated with reduced open-water nocturnal activity.

As pointed out in Chapter IV, recently-hatched fish are positively phototropic and show a fairly continuous pattern of activity. However, the activity cycle of a fish of total length 29 mm (see Fig. 37), taken from a quiet stretch of the River in January 1971 indicates that G. vulgaris soon becomes predominantly nocturnal. The diel activity ratio of this fish was 4.6: similar ratios of 3.7 and 4.1 were recorded for a further two juvenile fish, 29 and 31 mm long respectively, taken from the River Glentui in January 1972.

Diel activity rhythms have been reported for a wide range of species inhabiting running water (see Spencer, 1929b, 1939; Hynes, 1970a:312). A number of workers (e.g. Swift, 1964; Chaston, 1968b; Campbell, 1971) have indicated that light is the most important external

factor affecting these rhythms, whilst Andreasson (1969) indicated the importance of temperature on the level of activity in the sculpins Cottus poecilopus and Cottus gobio. That the timing of the diel activity cycle may not be entirely exogenous is indicated by the work of Andreasson and Muller (1969) on C. poecilopus. This species shifts activity phase from dark-activity to light-activity during the year. Some specimens were taken from a location at latitude 66° N and studied in that area, whilst others were transferred to a location at latitude 55° N. This latter group, after six months maintenance in natural light conditions, showed a phase shift that was simultaneous with that of the fish at 66° N. Fish caught at 55° N and studied there showed no phase shift.

Light appeared to be the most important external factor affecting the activity of G. vulgaris (see Fig. 36). On three occasions, continuous recordings were made of both the air and water temperatures in the activity aquarium. Although changes in the air temperature followed closely the cycle of light, changes in water temperature tended to lag behind and were not correlated with changes in intensity of activity. However, under natural conditions it is probable that seasonal temperature differences affect the level of activity. Lack of facilities prevented the simultaneous investigation of the spontaneous locomotory activity of different age groups, although age has been shown to have an effect on both the level of activity and its periodicity in a number of species (Spencer, 1939). The latter fact does not detract from the findings presented in Table 34 and Fig. 36 in which, irrespective of age, only fish tested in August and September had diel activity ratios less than 1.

Swift (1962, 1964), working on the relationship between feeding and activity of S. trutta, concluded that the trout "feeds because it is active, and is not active because it is feeding." However, as pointed out by Hynes (1970a:313) swimming activity may not necessarily be associated with feeding. In G. vulgaris, feeding was found to be dependent on activity and did not occur when the fish remained hidden under and between boulders.

4. The Diets of the Other Fish Species Inhabiting the River Glentui

The diets of P. breviceps, S. trutta and Anguilla spp. are presented in Figs. 38 (February 1971), 39 (May 1971) and 40 (November

Key to food organisms listed in Figs. 29, 30, 32, 33, 34, 38, 39 and 40. (L = larvae, P = pupae, A = adults).

1. Archichauliodes diversus L.
2. plecopteran L. (Stenoperla, Zelandoperla, Aucklandobius spp.).
3. Coloburiscus humeralis L.
4. Nesameletus sp. L.
5. Deleatidium spp. L.
6. other ephemeropteran L. (Oniscigaster, Zephlebia spp.).
7. ephemeropteran and trichopteran A.
8. Hydropsyche colonica L.
9. Hydrobiosis sp. L.
10. Olinga sp. L.
11. Pycnocentrodes sp. L.
12. other cased trichopteran L. (Helicopsyche, Hudsonema, Beraeoptera, Triplectides, Oxyethira).
13. chironomid L, P, A. (Orthocladiinae, Tanytarsini, Anatopynia, Maoridiamesa harrisi).
14. simuliid L, P, A. (Austrosimulium ungulatum, Austrosimulium multicorne).
15. other aquatic dipterans (Dixidae, Tabanidae, Tipulidae).
16. aquatic Coleoptera (mainly elmid A, L.).
17. Potamopyrgus antipodarum.
18. terrestrial Arthropoda (mainly Hymenoptera, Coleoptera, Lepidoptera, Orthoptera and Diptera).
19. Vertebrata (mainly P. breviceps, S. trutta, G. vulgaris)
20. others (mainly lumbricids, plant material, aquatic Hemiptera).

FIGURE 38. Diets of G. vulgaris (G), P. breviceps (P), S. trutta (S) and Anguilla spp. (A) in the River Glentui in February 1971. (Sample sizes : G. vulgaris = 50, P. breviceps = 124, S. trutta = 38, Anguilla spp. = 38).

The key to the food organisms (numbered 1 - 20) is on the blue fold-out page.

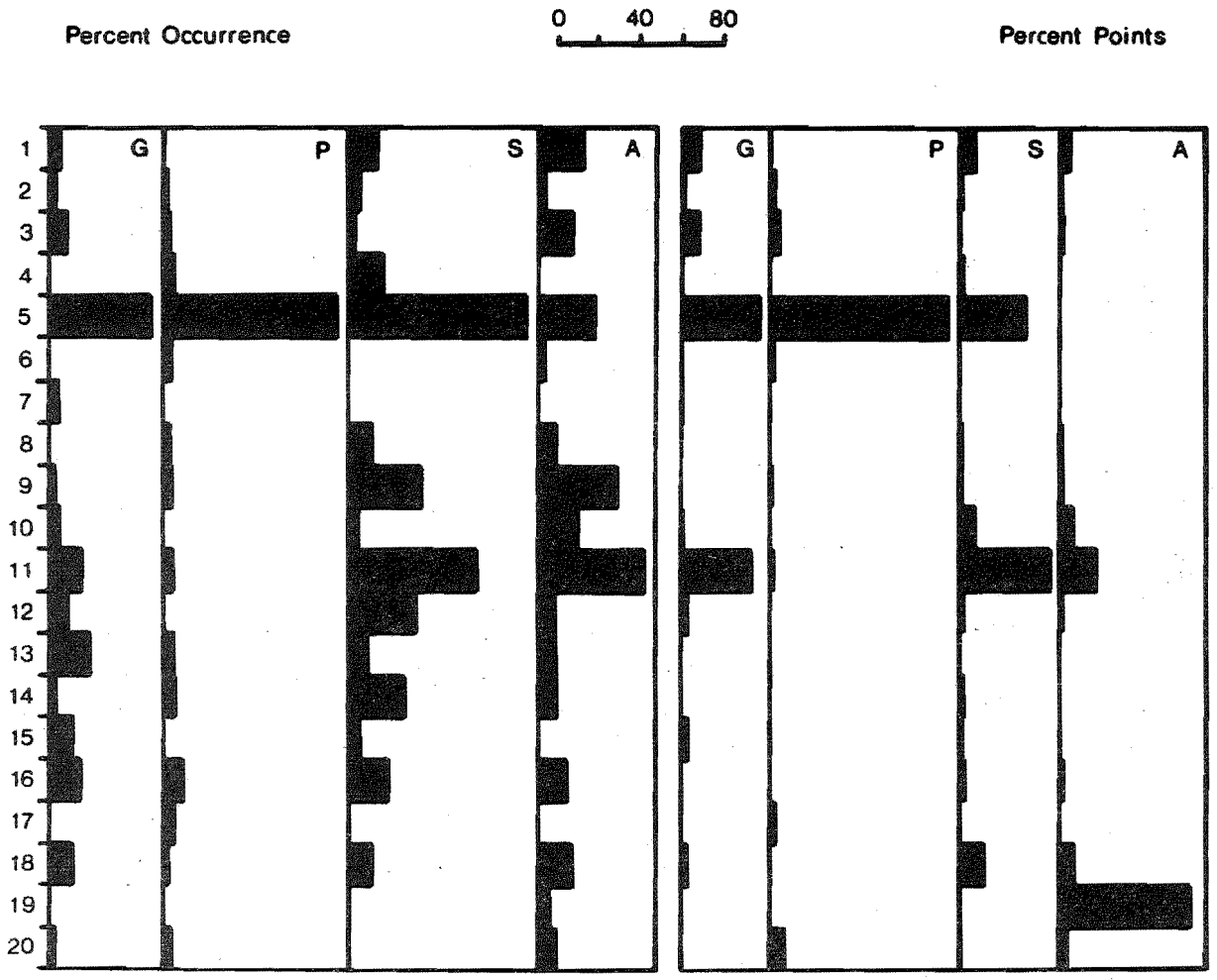

Percent Occurrence
0 40 80
Percent Points
G
P
S
A
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20

FIGURE 39. Diets of G. vulgaris (G), P. breviceps (P), S. trutta (S) and Anguilla spp.(A) in the River Glentui in May 1971. (Sample sizes : G. vulgaris = 69, P. breviceps = 152, S. trutta = 38, Anguilla spp. = 18).

The key to the food organisms (numbered 1 - 20) is on the blue fold-out page.

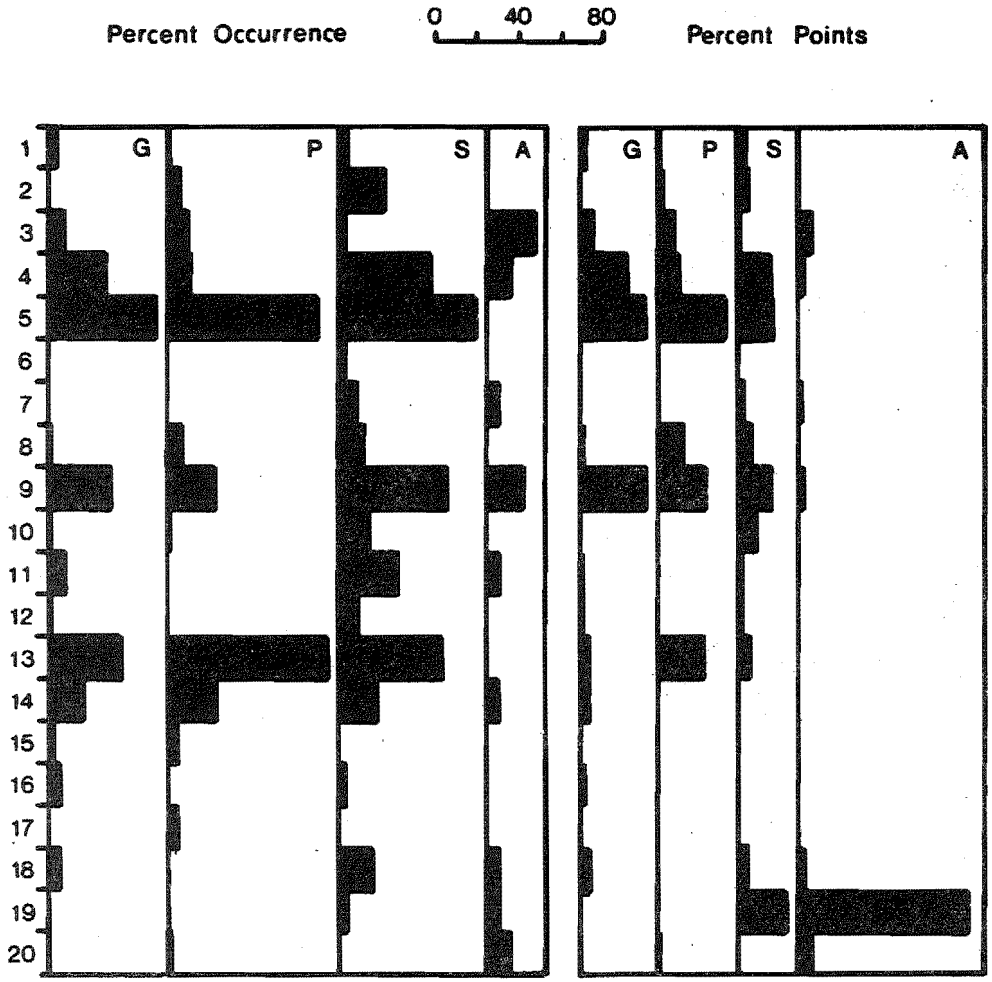
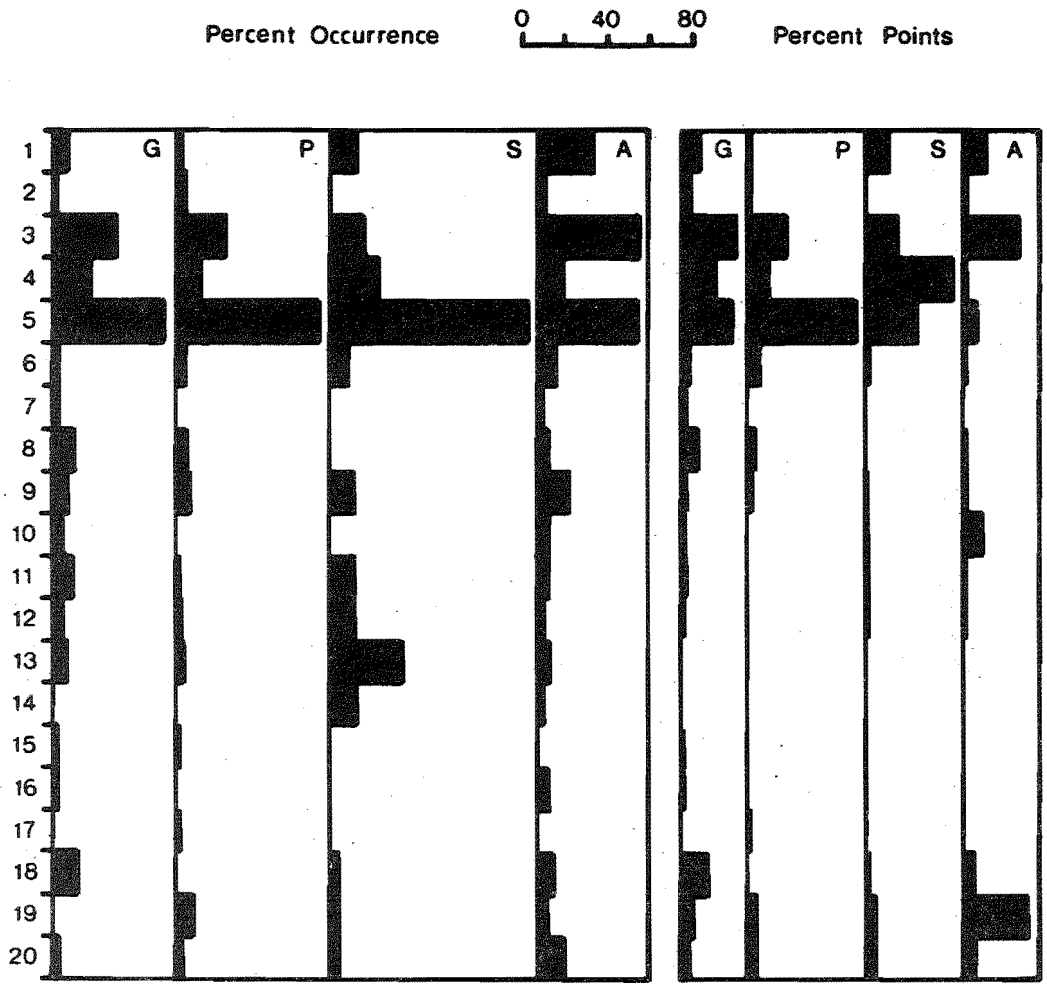

Percent Occurrence
0
40
80
Percent Points
G
P
S
A
G
P
S
A
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20

FIGURE 40. Diets of G. vulgaris (G), P. breviceps (P), S. trutta (S) and Anguilla spp. (A) in the River Glentui in November 1971. (Sample sizes: G. vulgaris = 168, P. breviceps = 154, S. trutta = 27, Anguilla spp. = 44).

The key to the food organisms (numbered 1 - 20) is on the blue fold-out page.


Percent Occurrence
0
40
80
Percent Points
G
P
S
A
1
2
3
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5
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7
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1971). The February and May samples were taken between 0900 and 1700 hours, whilst the November sample was taken over a 24-hour period. Details of the fish in each sample are presented in Table 35. Because of the small numbers of A. australis found in the River, samples of A. australis and A. dieffenbachii were combined for subsequent analyses. Cairns (1942, 1950) indicated that there was little difference between the diets of the two species of eel.

TABLE 35. Details of the fish in each of the samples used to investigate the diets of P. breviceps, S. trutta and Anguilla spp. (n = sample size; n.e. = number of empty stomachs in each sample; $\bar{sy}$ = standard error of the mean; L = A. dieffenbachii; S = A. australis; i = large trout; ii = small trout).

				length (mm)			
	Sample	n	n.e.	min.	max.	mean	$\bar{sy}$
P. breviceps	Feb.	124	8	40	85	55	0.93
	May	152	5	38	90	63	0.81
	Nov.	154	30	48	87	67	0.83
S. trutta	Feb.	38	2	72	292	97	5.36
	May	33	1	82	310	136	6.48
	Nov. i	8	0	134	202	160	8.08
	Nov. ii	19	0	42	50	46	0.54
Anguilla spp.	Feb. L	35	13	210	1000	348	24.63
	Feb. S	3	1	93	340	211	58.39
	May, L	18	8	200	780	410	38.31
	Nov. L	36	7	120	880	306	23.64
	Nov. S	8	6	105	330	168	26.90

(1) P. breviceps

Hopkins (1965, 1970, 1971b) examined the food of stream-dwelling P. breviceps and reviewed (Hopkins, 1965) the sparse literature on the food of bullies, of the genera Gobiomorphus and Philypnodon, in New Zealand. Staples (1971, unpublished) recorded the diet of P. breviceps in a small mountain lake. Both authors noted differences in the diet of different size and age groups, whilst Staples (loc. cit.) recorded

TABLE 36. Diet of P. breviceps in different length-groups (in mm) assessed by both the percent occurrence and the percent points methods (February, May and November samples combined). (n = sample size; L = larva; P = pupa; A = adult).

	38–49 (n=58)		50–59 (n=155)		60–69 (n=105)		70–79 (n=72)		>80 (n=40)	
	% occ.	% pts.	% occ.	% pts.	% occ.	% pts.	%occ.	% pts.	% occ.	% pts.
Archichauliodes diversus L.			1.3	1.6	1.0	0.9				
Stenoperla sp. L.					1.0	0.9				
Zelandoperla sp. L.							1.4	0.8		
Aucklandobius sp. L.	3.4	0	1.3	0.8	4.8	0.9	2.8	1.5	2.5	0
Coloburiscus humeralis L.	3.4	6.3	4.5	7.0	14.3	12.4	23.6	24.2	20.0	8.7
Nesameletus sp. L.	6.8	0	9.0	10.9	8.6	8.8	6.9	3.9	15.0	5.8
Deleatidium spp. L.	74.2	84.4	72.3	65.1	66.7	37.2	72.2	41.4	70.0	52.2
Oniscigaster sp. L.					1.0	2.7			5.0	8.7
Zephlebia sp. L.	1.7	0			2.8	1.8	2.8	0.8		
Hydropsyche colonica L.	3.4	0	2.6	2.3	6.7	6.2	6.9	6.3	7.5	5.8
Hydrobiosis sp. L.	5.1	0	6.5	3.9	16.2	11.5	12.5	8.6	17.5	7.2
Olinga sp. L.					1.0	0				
Pycnocentrodes sp. L.	3.4	3.2	1.3	0.8	1.0	0			2.5	0
Beraeoptera sp. L.					1.0	0				
Triplectides sp. L.									2.5	0
tipulid L, P.			1.8	0	4.0	0	1.7	0		
chironomid L, P.	15.5	0	34.3	6.2	34.6	11.5	25.0	3.1	27.4	2.9
simuliid L, P.	1.7	0	8.5	0	11.4	0	16.3	0	10.1	0
elmid L, A.	1.7	0	3.9	0	2.9	0				
Potamopyrgus antipodarum	1.7	0	0.6	0	3.8	0.9	5.6	1.6	12.5	0
P. breviceps eggs			1.3	0.8	1.9	0.9	2.8	0.8	12.5	8.7
terrestrial arthropods			0.6	0	1.0	0				
terrestrial lumbricids	3.4	6.3	0.6	0.8	3.8	3.5	2.8	7.0		

seasonal changes in the diet within each age group.

In the River Glentui, ephemeropteran larvae, particularly Deleatidium spp., and to a less extent Nesameletus sp. and Coloburiscus humeralis, were the most important items in the diet of P. breviceps: the larvae of Zephlebia sp. and Oniscigaster sp. were rarely eaten and were found in only six and two stomachs of the 430 examined, respectively. Free-living trichopteran larvae (Hydropsyche colonica and Hydrobiosis sp.) were also important items in the diet, particularly in May: cased-caddis larvae were taken only occasionally and were regarded as incidental items. Of the aquatic dipteran larvae, chironomids were found in large numbers in May, and although they were found in the other two samples they occurred in only a few stomachs (five in February, four in November). Similarly, simuliid larvae, although occurring in 31 stomachs in May, did not form a substantial part of the diet, on a points basis: tipulid larvae and the pupae of chironomids, simuliids and tipulids occurred infrequently (4, 1, 3 and 4 stomachs respectively). Plecopteran larvae, particularly Aucklandobius sp., were found in a few stomachs in each sample. Elmid adults and larvae were found only in the February sample, in 10 stomachs. Potamopyrgus antipodarum was found in all samples, although it occurred in only a few stomachs (see Figs. 38, 39 and 40). Terrestrial arthropods were taken by only two fish, whilst lumbricids of terrestrial origin were found in six stomachs. In the February sample, 72 P. breviceps eggs were found in the stomachs of 11 fish and constituted 4.2% of the diet, on a points basis, for that month.

Similarly, Hopkins (1965) recorded Deleatidium sp. as the most important food item for adult P. breviceps, 50-80 mm long. First-year fish, 20-40 mm long were found to feed mainly on chironomids, Deleatidium sp. and Paracalliope fluviatilis, an amphipod not found in the River Glentui sampling area. Although P. breviceps smaller than 38 mm were not sampled in the present study, there was some indication that the diet of fish smaller than 50 mm differed somewhat from the diet of larger fish.

The diets of P. breviceps in different length groups are presented in Table 36, in which it may be seen that there is little difference in the

composition of the diets assessed by the occurrence method. This is confirmed by the Kendall rank correlation coefficients between the diets of all length groups: all coefficients indicate similarity ($p < 0.01$). However, Kendall rank correlation coefficients for comparisons of the diets assessed by the points method indicate that the diet of fish in the smallest length group, viz. 38 - 49 mm, differed significantly ($p > 0.05$) from the diet of fish in all other length groups, except the 70 - 79 mm group ($p = 0.01 - 0.001$): all other length-group comparisons revealed similarity ($p < 0.05$) of diets.

(2) S. trutta

The diet of S. trutta inhabiting both lotic and lentic habitats has been well documented by a large number of workers in various parts of the world (see e.g. Allen, 1938; Idyll, 1942; Butcher, 1945; Nilsson, 1957, 1967a; Ball, 1961; Horton, 1961; McCormack, 1962; Thomas, 1962; Elliott, 1967c, 1970; Frost and Brown, 1967; Chaston, 1968c; Tusa, 1968, 1969; Carlander, 1969; Hunt and Jones, 1972). Similarly, in New Zealand the food and feeding habits of brown trout have been the subjects of a number of investigations (see e.g. Phillipps, 1924; Phillips, 1929; Percival, 1932; Allen, 1951; Lane, 1964; Hopkins, 1965, 1970, 1971b; Burnet, 1963, 1969a).

In the present study the most important food items in the diet of S. trutta were found to be ephemeropteran larvae, particularly Deleatidium spp. and Nesameletus sp., and to a less extent C. humeralis. Zephlebia sp. and Oniscigaster sp. were taken only rarely. Adult Ephemeroptera were found in three stomachs in May. Larvae of the cased trichopteran Pycnocentrodes sp., were also important in the diet, whilst Olinga sp., Beraeoptera sp., Hudsonema sp., Triplectides sp. and Oxyethira sp. were taken occasionally. The free-living larvae of H. colonica and Hydrobiosis sp. were common in the May sample, but were found less frequently in February and November. Aquatic dipteran larvae were important constituents of the diet of the smaller trout (< 50 mm). Chironomid larvae were frequently taken, whilst simuliid and tipulid larvae were found occasionally. Chironomid pupae were found in one stomach out of 98 examined. Larvae of the neuropteran A. diversus were found in nine stomachs and formed a substantial part of the stomach contents of those fish in which it occurred.

TABLE 37. The diet of "large" and "small" S. trutta sampled in the River Glentui in November 1971. (Figures in parenthesis are the numbers of individual Deleatidium spp. larvae).

	"large" fish, n = 8 mean length = 160mm (S.E. ± 8.08).			"small" fish, n = 19 mean length = 46mm (S.E. ± 0.54)		
	occ.	points	% points	occ.	points	% points
Archichauliodes diversus L.	3	19	11.7			
Coloburiscus humeralis L.	4	27	16.6			
Nesameletus sp. L.	6	77	47.2			
Deleatidium spp. L.	6	21 (85)	12.9	19	25 (122)	92.6
Oniscigaster sp. L.	1	1	0.6			
Zephlebia sp. L.				1	1	3.7
Hydrobiosis sp. L.				3	1	3.7
Olinga sp. L.	1	1	0.6			
Pycnocentrodes sp. L.	3	3	1.8			
Hudsonema sp. L.	2	3	1.8			
Beraeoptera sp. L.	1	0				
Triplectides sp. L.	1	2	1.2			
chironomid L.	1	0		8	0	
terrestrial arthropods	1	1	0.6			
Pisces (P. breviceps)	1	8	4.9			

The plecopteran larvae Aucklandobius sp. and Stenoperla sp. were found in six and three stomachs respectively. Elmid larvae and adults were found on a few occasions (see Figs. 38, 39 and 40). Terrestrial arthropods were found in 10 stomachs and normally formed the major constituent of the stomach contents of the fish in which they occurred. Two trout were found to have eaten fish; one, 19 cm long, contained the anterior third of a P. breviceps, whilst another, 21 cm long, contained a whole P. breviceps of about 43 mm in length. Plant material, in the form of a small twig, occurred in only one stomach.

Although basically the same food items occurred in each sample, the relative proportions of each item in the diet of S. trutta varied greatly between the three samples (see Figs. 38, 39 and 40). The variation in the diet was also indicated by the Kendall rank correlation coefficients between samples, all of which indicated dissimilarity ($p > 0.05$) when comparisons were made using the points assessments (for February and May, $\tau = 0.0704$, $z = 0.3656$; for February and November, $\tau = 0.1588$, $z = 0.8254$; for May and November, $\tau = 0.2816$, $z = 1.4634$). Although the November sample was taken over a longer period than the other two samples and the differences between samples probably reflect, to some extent, seasonal variation in the availability of food organisms, it appears that the difference in mean size of the fish in each sample played an important role in producing the observed variation. That size is an important factor in determining the diet of brown trout in the River Glentui is indicated by the November sample (see Table 35), which consisted of one group of eight large fish of mean length 160 mm (s.e. $\pm$ 8.08) and another group of 19 small fish of mean length 46 mm (s.e. $\pm$ 0.54). The diets of the two groups are presented in Table 37. Even though the sample size of the "large" fish is small, it may be seen that they took a greater variety of food organisms than the "small" fish did. All of the organisms eaten by the "large" fish, except the larvae of Deleatidium spp., Beraeoptera sp. and chironomids, were too large to be eaten by the "small" fish. Furthermore, there is some indication that the "large" fish took larger individuals of Deleatidium spp. larvae than "small" fish; in "large" fish, 4.1 (85/21) larvae were required to merit one point, whereas in "small" fish 4.9 (122/25) larvae were required.

(3) Anguilla spp.

As pointed out by Cairns (1942) and Burnet (1952), the feeding habits of A. australis and A. dieffenbachii are generalized and readily adaptable to most faunas. These conclusions are substantiated by the observations of Hopkins (1965, 1970, 1971b). Similarly, in the present study, Anguilla spp. were found to take a wide variety of food organisms. Their large size (see Table 35) enabled them to take individual food items which were much larger than those taken by the other fish in the River, with the exception of a few large trout. A notable feature of the eel samples taken in the River Glentui was the number of empty stomachs recorded (36.8, 44.4 and 29.5% of the eels in the February, May and November samples respectively). Burnet (loc. cit.), working with A. dieffenbachii, noted that there was a tendency for the number of empty stomachs to increase with increasing eel size and suggested that large eels probably feed less frequently than small eels. Cairns (loc. cit.) found that eels feed spasmodically, often taking large amounts of food and then resting while it is digested.

In the River Glentui, larvae of Ephemeroptera, particularly C. humeralis, Deleatidium spp. and Nesameletus sp., Rhyacophilidae (Hydrobiosis sp.), A. diversus and the cased Trichoptera, Olinga sp. and Pycnocentrodes sp., occurred frequently in the stomach contents. Vertebrates were taken less frequently, but when they occurred they formed a substantial part of the stomach contents. On one occasion a mouse, Mus musculus, was found in the stomach of an eel 560 mm long. Four stomachs contained the remains of fish: in one instance, a trout approximately 140-150 mm long was found in the stomach of an eel 460 mm long: four G. vulgaris, 92, 77, 72 and 51 mm long, were found in the stomach of an eel 560 mm long: a trout approximately 170 mm long, part of the skull of a trout and the remains of what appeared to be a number (c. 10) of small P. breviceps (< 50 mm) were found in the stomach of an eel 1,000 mm long, and another eel 220 mm long had eaten 60 P. breviceps eggs.

Other items eaten included terrestrial arthropods and lumbricids (found in 10 and 3 stomachs respectively) and the larvae of Stenoperla sp. (Plecoptera), Zephlebia sp. and Oniscigaster sp. (Ephemeroptera), H. colonica, Beraeoptera sp., Triplectides sp., and Oxyethira sp.

TABLE 38. Kendall rank correlation coefficients for interspecific comparisons of the diet of G. vulgaris, P. breviceps, S. trutta and Anguilla spp. (A. dieffenbachii and A. australis combined) at three different times of the year (1971): (a) February (sample sizes: G. vulgaris = 50, P. breviceps = 124, S. trutta = 38, Anguilla spp. = 38). (b) May (sample sizes: G. vulgaris = 69, P. breviceps = 152, S. trutta = 33, Anguilla spp. = 18). (c) November (sample sizes: G. vulgaris = 163, P. breviceps = 154, S. trutta = 27, Anguilla spp. = 44). Figures in parenthesis are values of z for testing the significance of τ. All comparisons are made between diets assessed by the points method.

	(a) February			(b) May			(c) November		
	G. vulgaris	P. breviceps	S. trutta	G. vulgaris	P. breviceps	S. trutta	G. vulgaris	P. breviceps	S. trutta
P. breviceps	0.1861 (0.9670)	-	-	0.6093 (3.1661)**	-	-	0.3757 (1.9524)	-	-
S. trutta	0.5140 (2.6706)**	0.0000 (0.0000)	-	0.2122 (1.1024)	0.4234 (2.2001)*	-	0.4256 (2.2113)*	0.4752 (2.4689)*	-
Anguilla spp.	0.2463 (1.2797)	-0.0591 (-0.3072)	0.2653 (1.3786)	0.3015 (1.5666)	-0.1127 (-0.5855)	0.5010 (2.6032)**	0.3201 (1.6631)	0.2769 (1.4385)	0.4977 (2.5861)**

* probability 0.05 - 0.01
** probability 0.01 - 0.001

Trichoptera), and chironomids and simuliids (Diptera). Elmid adults were taken on a few occasions (see Figs. 38, 39 and 40). Adult Trichoptera were found in two stomachs, whilst Gordius pachydermus was found in the stomach of three eels. Terrestrial plant material, in the form of leaves, buds, twigs and pieces of bark, occurred in six stomachs.

5. Comparison of the Diets of the Fish Species in the River

The diets of G. vulgaris, P. breviceps, S. trutta and Anguilla spp., assessed by both the occurrence and points methods and discussed in previous sections, are presented for comparison in Figs. 38, 39 and 40. With few exceptions, the same food organisms were utilized by all species, with the larvae of Deleatidium spp. forming a substantial part of the diet of three out of the four species (A. australis and A. dieffenbachii being considered as one). However, the relative proportions of each item in the diet, particularly on the points assessment, tended to vary between species. For example, fish were more important in the diets of S. trutta and Anguilla spp. than in the diets of G. vulgaris and P. breviceps, and the larvae of Pycnocentrodes sp. were rarely found in P. breviceps stomachs, whereas they often formed a substantial part of the diets of Anguilla spp., G. vulgaris and S. trutta. Similarly, terrestrial arthropods occurred frequently in the stomachs of G. vulgaris, S. trutta and Anguilla spp., but occurred only rarely in P. breviceps stomachs, whereas Potamopyrgus antipodarium was found only in P. breviceps stomachs

Since sample sizes, particularly of S. trutta and Anguilla spp., were relatively small (< 50), it was considered that more accurate assessments of the relative importance of the various items in the diets were provided by the points method (see section 1.(2) in this Chapter). Kendall rank correlation coefficients for comparisons of the diets of all species were therefore calculated using only the results obtained by the points method. The coefficients (see Table 38) indicate that the diets of the native species in the River Glentui were dissimilar, with the exception of the diets of G. vulgaris and P. breviceps in May. However, in six out of nine comparisons involving the introduced S. trutta, the coefficients indicate varying degrees of similarity ($p < 0.05$) between the diet of the trout and the diets of the native species. The implications

of these similarities are discussed in Chapter VII.

6. Nematode Relationships

During the investigation of food habits, parasitic nematodes were found in the alimentary canal and liver of P. breviceps and Anguilla spp. Of the 24 P. breviceps in which nematodes were found, 22 were females. No nematodes were found in G. vulgaris or S. trutta. No specific search was made for parasites, other than a close examination of the stomach contents of each fish. The nematodes were identified by Thomas (pers. comm.).

The nematodes from the alimentary canal of Anguilla spp. (both A. dieffenbachii and A. australis) were male anisakids, characterized by the possession of three lips and interlabia, lips with dentiferous ridges, an excretory pore at the base of the ventral interlabium and an oesophagus with a ventriculus. They belong to either Paranisakis (= Paranisakispis) or Ichthyanisakis, probably the former. Brunsdon (1956, unpublished) reported an encysted larva of Paranisakis sp. in the stomach wall of A. dieffenbachii. A further group of nematodes from the stomach of A. dieffenbachii were tentatively identified as Eustrongylides or Philometra, both of which have been found previously in A. dieffenbachii (Brunsdon, loc. cit.; Hewitt and Hine, 1972).

The nematodes from the liver and body cavity of P. breviceps were larval stages of an anisakid, possibly the younger stage of the anisakids found in the eels. They were characterized by a ventral larval tooth, no lips, an oesophagus with a terminal ventriculus, no alimentary appendages, and an excretory pore near the head.

It is the habit of larval anisakids to occur in the body cavity or liver and to grow to the adult in the gut of a fish, or higher vertebrate, which eats the larval host. The eggs are shed in the faeces of the final host (Thomas, pers. comm.). Since eels in the River Glentui were found to eat P. breviceps, albeit only occasionally, it is possible that the anisakid life history is completed within the River. The mollusc Potamopyrgus antipodarum seems the most probable intermediate host, since as a detritus-feeder (Winterbourn, pers. comm.) it is likely to feed on the faeces of eels. Furthermore, it was found in the diet of P. breviceps in the River Glentui, but was not found in the stomach contents of G. vulgaris and S. trutta, neither of which contained nematodes

in their stomachs.

7. The Relationship Between the Invertebrate Drift Fauna and the Feeding Habits of G. vulgaris and P. breviceps over a 24-hour Period

Since the work of Muller (1954), the concept of drift and its significance to the stream ecosystem has received a great deal of attention (see e.g., Elliott, 1965, 1967a, b, 1971; Waters, 1965, 1969; Bishop and Hynes, 1969; Hynes, 1970a, b; McLay, 1970; Elliott and Corbett, 1972). Diel periodicity in the drift is found to be common in most of the species of invertebrates which have been studied; most are night-active but some are day-active (Waters, 1962, 1968; Muller, 1963; Levanidova and Levanidov, 1965; Madsen, 1966; Anderson, 1967). Light intensity and water temperature appear to be the major external factors controlling the pattern of night-activity and day-activity respectively, whilst the magnitude of the drift appears to depend on a number of factors, including water temperature, current velocity, stage of life cycle, population density and behaviour, acting singly or in combination (Anderson, 1966; Dimond, 1967; Holt and Waters, 1967; Chaston, 1968a; McLay, 1968; Minshall and Winger, 1968; Pearson and Franklin, 1968; Waters, 1968, 1969; Bishop, 1969; Hughes, 1970; Lehmkuhl, 1972; Lehmkuhl and Anderson, 1972).

In New Zealand, McLay (1968), working in the Kakanui River, recorded diel periodicity in the overall drift rate with maximum rates just after sunset. Comparatively large numbers of ephemeropteran nymphs and Rhyacophilidae (Hydrobiosis spp.) were found to occur in the drift at night. Similarly, Watson (1971) recorded relatively large numbers of ephemeropteran and trichopteran larvae in the drift of a small stream in the Auckland province. Burnet (1963, 1969a) working in the South Branch of the Waimakariri River, Canterbury, found that overall drift rate was at a maximum at night. Fowles (1972, unpublished), working in the same locality, recognized distinct night-active, day-active and intermediate species. McLay (1970) developed a model of stream drift and demonstrated its applicability to previously published experiments. The model has received further support from the work of Ogilvie (1971, unpublished).

The significance of drifting invertebrates to stream fish lies in

an increase in the availability of food. As pointed out by Waters (1969), this may occur in two ways. Firstly, drift may carry invertebrates from the area of their production to an area where they may be consumed and, secondly, drifting invertebrates may be more visible and therefore more available to fish such as salmonids in which visual stimulation is an important factor in feeding (Chapman, 1966). A number of workers have indicated the importance of drift as fish food (Norback, 1884, quoted by Kalleberg, 1958; Needham, 1929; Nilsson, 1957; Mason and Chapman, 1965; Bishop and Hynes, 1969; Mann and Orr, 1969; Mason, 1969) and have observed fish actually feeding on drift (Muller, 1954; Horton, 1961; McCormack, 1962). Elliott (1967c), working with S. trutta, concluded that the availability of many benthic animals increases at night and that the trout use this readily available food either as drift or from the tops of stones. On the other hand, Chaston (1968c), studying the feeding of S. trutta in an experimental situation, suggested that only terrestrial material is utilized, whilst the aquatic component of invertebrate drift is not exploited as a food source. White (1966, quoted by Waters, 1969), Elliott (1970) and Jenkins, Feldmeth and Elliott (1970), comparing fish stomach contents with drift at different times of the day, recorded larger proportions of drifting organisms in the stomachs at the same times that their drift was high. That fish are capable of feeding on drift at night is indicated by the observations of Jenkins (1969), who introduced marked ants into the drift in experimental stretches of a rocky-substrate stream and examined the stomachs of brown and rainbow trout for the presence of marked ants immediately after the last ant had been introduced. Both species of trout were found to feed on the ants at night, although to a less extent than they did during the day. Similarly, Tanaka (1971), working in an experimental stream tank, concluded that rainbow trout are capable of feeding on drifting insects at night.

To examine the relationships between the fish species and the invertebrate drift fauna in the River Glentui, a series of simultaneous samples was taken of both drift and fish from 1500 hours on 12-11-71 to 1500 hours on 13-11-71.

(1) Methods

The invertebrate drift fauna was sampled hourly throughout the

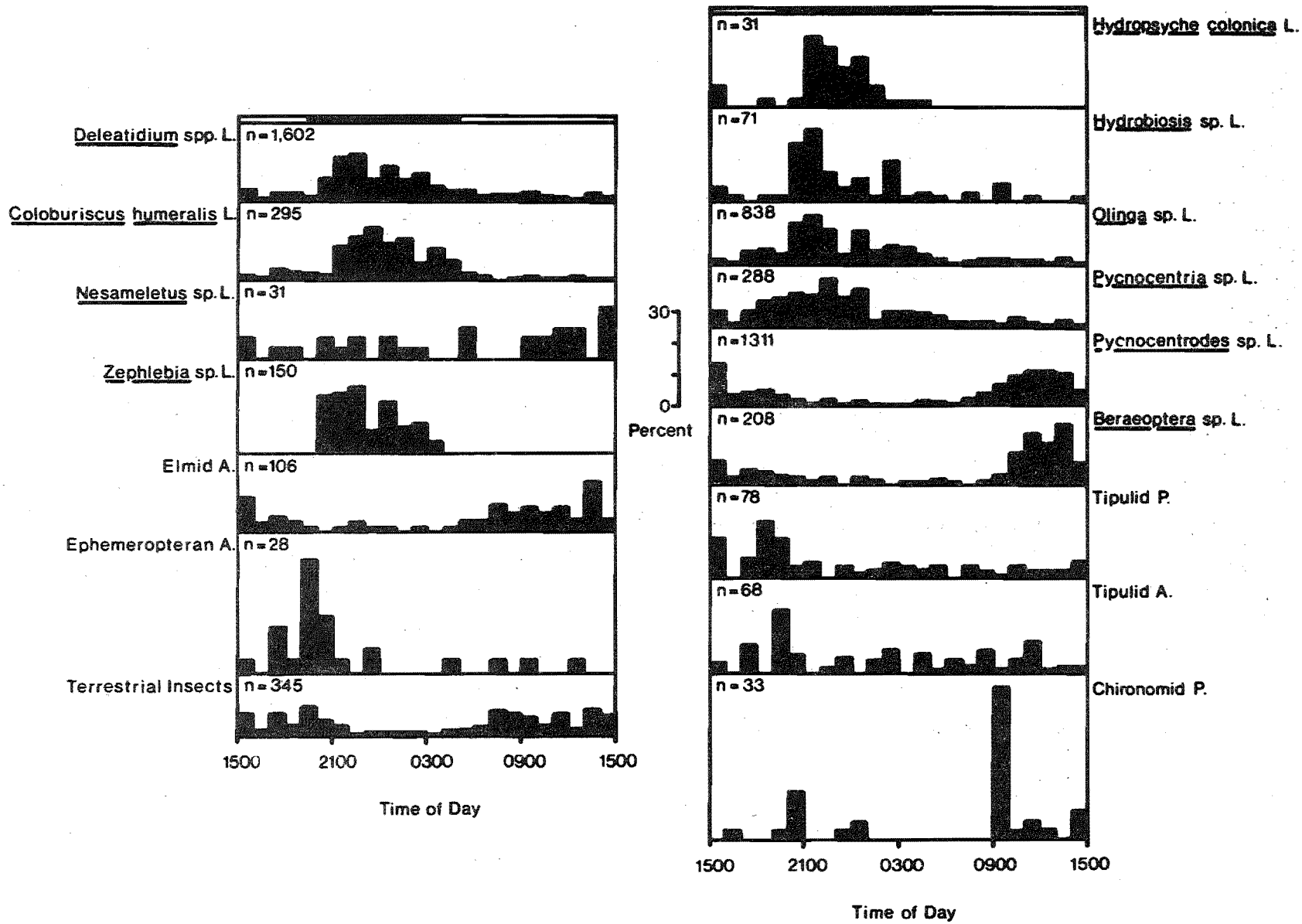
24-hour period using two Brundin nets (Brundin, 1966: 73). The nets were cone-shaped with a circular opening (32 cm diameter; 0.08 m^2 in area) leading into a tapered collecting net (0.5 mm mesh; 16 meshes/cm) (Fowles, 1972 unpublished). Each net was positioned in the River by means of three short cords, attached equidistantly around the opening, and joined in front of the net to a long central cord which was attached to a boulder on the river bed. One net was used in each sampling period, at the end of which it was replaced by the other. The nets were arranged so that all samples were taken at the same point, in the middle of a riffle area, where the water current was sufficient to maintain the nets in position with only a small part of their circumference touching the river bed. The liklihood of benthic invertebrates crawling into the net was thereby reduced.

The 24 hourly samples were preserved in 5% formalin and sorted at a later date. No quantitative bottom samples were taken.

The fish species in the River were sampled by electric fishing every four hours, with each sampling period extending one hour on either side of the sample time. For example, the sampling period for the 0800 hours collection extended from 0700 to 0900 hours, with 10 minutes out of each hour for changing over the drift nets. After capture, fish were immediately anaesthetized and preserved in 10% formalin. Stomach contents were later assessed by both the occurrence and the points methods, and the dry weight of food in each sample of each species was obtained and related to the total wet weight of the fish in each sample. Since the object of this analysis was to determine the relative proportion of each food item taken at various times of the day, rather than a measure of the relative proportion of each item in the diet at any particular time, the total points allotted to each food item in each sample were converted to points per fish. The percent occurrence method is applicable to both types of analysis.

All fish samples were taken at least 0.8 km above the drift-sampling site. Although electric fishing has been shown to cause an increase in the number of invertebrates in the drift (Elliott and Bagenal, 1972), it was considered that the distances between the sampling sites for fish and drift were sufficient to prevent any artificially displaced

FIGURE 41. Diel periodicity of the major drifting invertebrates in the River Glentui between 1500 hours on 12-11-71 and 1500 hours on 13-11-71. Each histogram indicates the hourly occurrence in the drift as a percentage of the total number of individuals (n) taken throughout the sampling period. (L = larvae; P = pupae; A = adults). Time between sunset and sunrise is indicated by the shaded horizontal bar.


Deleatidium spp. L.
n=1,602
Coloburiscus humeralis L.
n=295
Nesameletus sp. L.
n=31
Zephlebia sp. L.
n=150
Elmid A.
n=106
Ephemeropteran A.
n=28
Terrestrial Insects
n=345
1500
2100
0300
0900
1500
Time of Day
30
0
Percent
n=31
Hydropsyche colonica L.
n=71
Hydrobiosis sp. L.
n=838
Olinga sp. L.
n=288
Pycnocentria sp. L.
n=1311
Pycnocentrodes sp. L.
n=208
Beraeoptera sp. L.
n=78
Tipulid P.
n=68
Tipulid A.
n=33
Chironomid P.
1500
2100
0300
0900
1500
Time of Day

organisms affecting the drift samples. This is supported by the observations of Elliott and Bagenal (loc. cit.) who, working in 20 and 40 m stretches of a stony stream, found that most of the invertebrates displaced from the upstream end of the experimental section returned to the bottom within the sampling area.

Hourly maximum and minimum water and air temperatures were recorded at the drift-sampling site.

(2) Results

(a) Drift

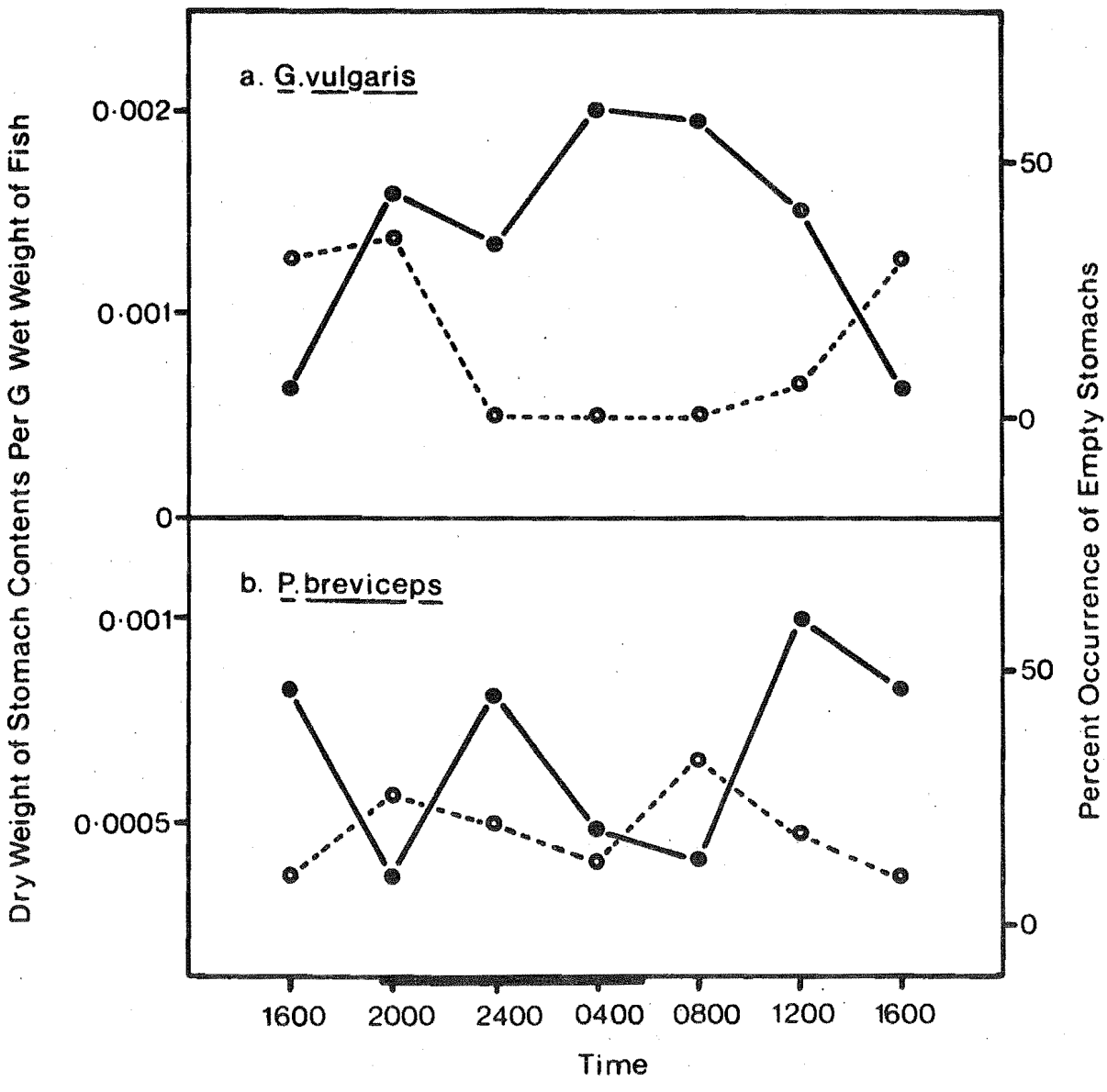
The drift patterns of the major drifting organisms are presented in Fig. 41. Larvae of Deleatidium spp., Zephlebia sp., Coloburiscus humeralis, Hydropsyche colonica, Hydrobiosis sp., Olinga sp., and Pycnocentria sp. were found primarily in the drift at night, with some forms showing a peak just after sunset. Terrestrial insects, elmid adults, chironomid pupae and the larvae of Pycnocentrodes sp. and Beraeoptera sp. occurred in the drift mainly during the day, with the chironomid pupae showing a mid-morning peak. Nesameletus sp. larvae and tipulid adults and pupae were found in the drift throughout the 24-hour period, although the tipulids, particularly the pupae, were found to be more frequent at dusk. Ephemeropteran adults occurred in the drift mainly at dusk.

Four larvae of Zelandoperla were found in the drift between 2100 and 2400 hours. Similarly, four larvae of Stenoperla were found between 2000 and 2300 hours. Thirteen chironomid adults were found in the drift, 10 between 0600 and 1300 hours and three between 1800 and 1900 hours. Twenty two individuals of G. pachydermus were taken in the drift nets during the 24-hour period, but showed no tendency to drift at any particular time of the day.

Other organisms found in the drift (with the number of individuals in parenthesis) included the larvae of Archichauliodes diversus (2), Helicopsyche sp. (8), Hudsonema sp. (2), Triplectides sp. (8), Ameletopsis sp. (1), chironomids (4), simuliids (5), dixids (8) and helodids (2); trichopteran adults (3); Anisops sp. (1) and Microvelia sp. (1).

Deleatidium spp. larvae were the most numerous items in the

FIGURE 42. Variation in the dry weight of stomach contents per gram wet weight of fish for G. vulgaris and P. breviceps sampled at four-hourly intervals over a 24-hour period in November 1971. The solid line represents the dry weight of stomach contents per gram wet weight of fish; the dashed line represents the percent occurrence of empty stomachs in each sample. Time between sunset and sunrise is indicated by the shaded portion of the X-axis.


a. G.vulgaris
b. P.breviceps
0·002
0·001
0
0·001
0·0005
50
0
50
0
Dry Weight of Stomach Contents Per G Wet Weight of Fish
Percent Occurrence of Empty Stomachs
1600
2000
2400
0400
0800
1200
1600
Time

drift during the sampling period and are the major drifting organisms in the River Glentui. (Ogilvie, pers. comm.).

Light intensity appeared to be the major factor controlling the periodicity of the night-active forms, whilst the occurrence in the drift of the aquatic day-active forms was correlated with water temperature (see Fig. 41 and Table 39), with increased occurrence in the drift associated with higher temperatures. Similarly, Waters (1968) recorded a positive correlation between water temperature and drift rate of the day-active larvae of Oligophlebodes sigma (Ephemeroptera).

TABLE 39. Product moment correlation coefficients (Sokal and Rohlf, 1969:498) between mean hourly water temperature and hourly occurrence in the drift of three day-active groups of invertebrates.

	r	95% CLs	
Pycnocentrodes sp. larvae	0.7805	0.5504	0.9004
Beraeoptera sp. larvae	0.7960	0.5782	0.9079
elmid adults	0.5680	0.2134	0.7903

(b) Diel variation in both feeding intensity and utilization of various food items by G. vulgaris and P. breviceps

Since insufficient numbers of S. trutta and Anguilla spp. were present in the sampling area, diel variation in the intensity of feeding in these species was not examined. Details of G. vulgaris and P. breviceps used in the present analysis are presented in Table 40. For each species, it may be seen that comparisons of all samples were made on groups of fish of similar size, thereby reducing any size-dependent variation in diet, feeding periodicity and feeding intensity, and providing the necessary basis for inter-sample comparisons of the points per fish for each food item.

The dry weights of the total stomach contents per gram wet weight of fish in each sample are presented in Fig. 42. Galaxias vulgaris was found to have a peak in dry weight of stomach contents at dusk and another peak later in the night, indicating two peaks of feeding. From the reduction in dry weight of stomach contents during the day, it was

TABLE 40. Details of G. vulgaris and P. breviceps sampled every four hours in the River Glentui over a 24-hour period in November 1971. (n = sample size; $s\bar{y}$ = standard error of the mean).

	Time	n	TL (mm) min.	max.	mean	$s\bar{y}$
G. vulgaris	1600	29	57	98	79	2.28
	2000	28	58	109	85	3.13
	2400	29	60	114	85	2.75
	0400	30	57	112	76	2.59
	0800	17	60	105	80	3.45
	1200	30	55	115	81	3.62
P. breviceps	1600	30	51	83	65	1.40
	2000	30	49	88	68	2.09
	2400	30	50	85	66	1.61
	0400	30	52	80	65	1.65
	0800	18	49	87	71	2.67
	1200	16	48	84	65	3.40

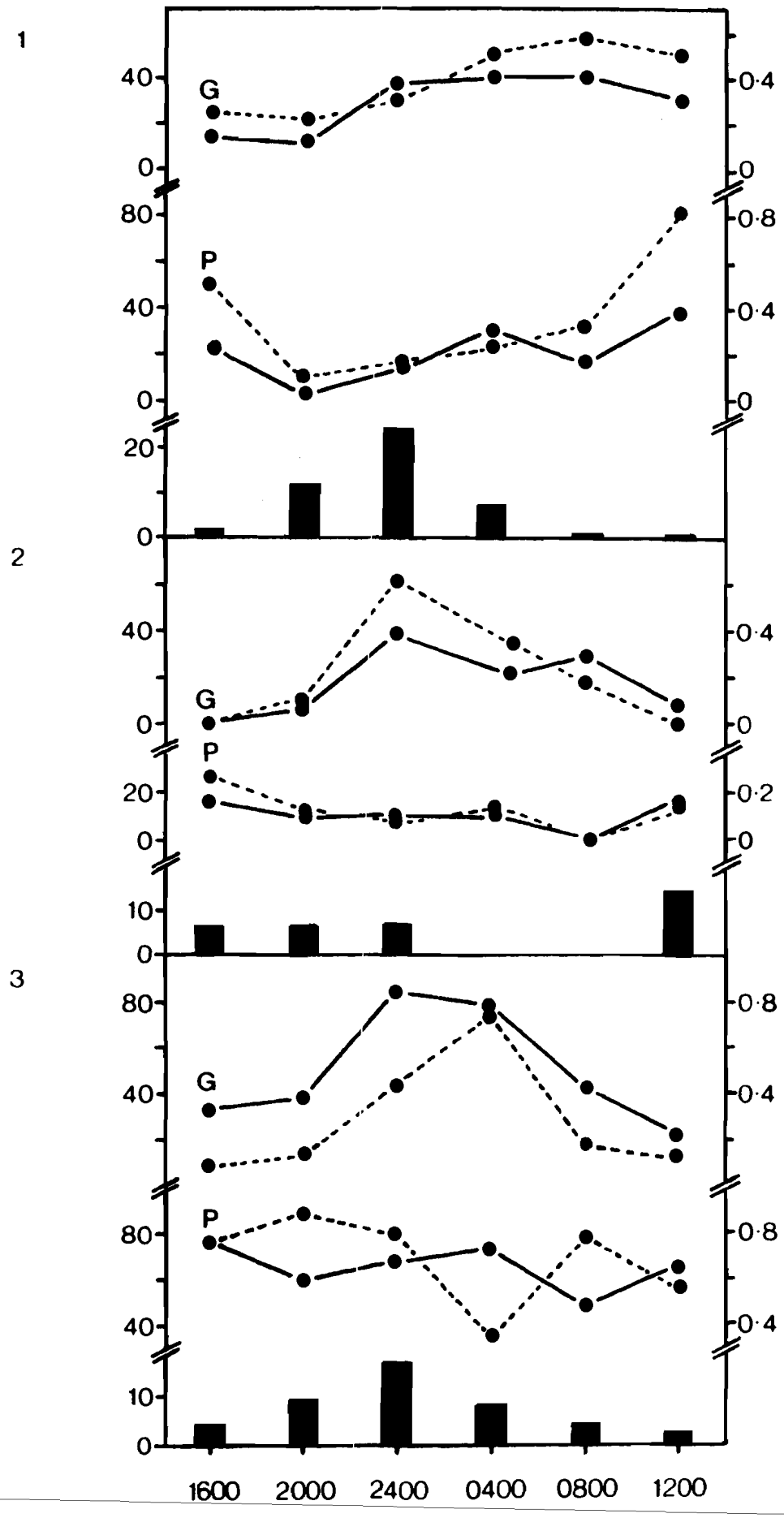
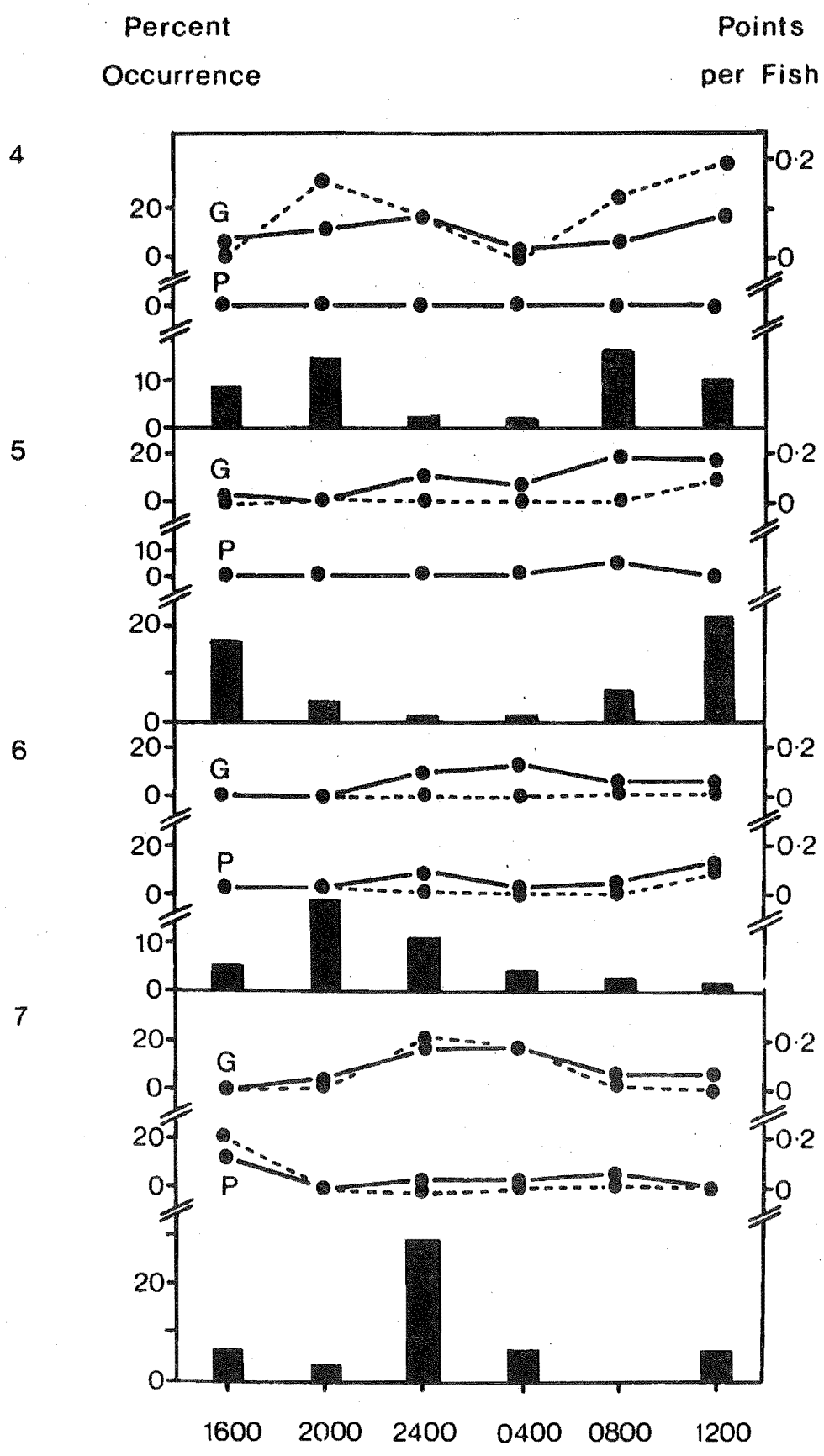

Percent
Occurrence
Points
per Fish
1
2
3
G
P
40
0
80
20
10
0·4
0·8
0·2
1600
2000
2400
0400
0800
1200

FIGURE 43. Percent occurrence (solid line) and points per fish (dashed line) for each of the major food items in the diets of G. vulgaris (G) and P. breviceps (P) at four-hourly intervals over a 24-hour period in November 1971. The proportion of each of the food items in the drift (as percentages of the total number of each item taken over the 24-hour period) during the time the fish samples were taken are presented in histogram form. The food items are:

1. Coloburiscus humeralis larvae.
2. Nesameletus sp. larvae.
3. Deleatidium spp. larvae.
4. terrestrial insects
5. Pycnocentrodes sp. larvae.
6. Hydrobiosis sp. larvae.
7. Hydropsyche colonica larvae.


Percent
Occurrence
Points
per Fish
4
5
6
7
G
P
20
0
10
0·2
1600
2000
2400
0400
0800
1200

assumed that G. vulgaris did not feed to any great extent during this period. The percent occurrence of empty stomachs was reduced to nil after the dusk feeding peak and increased throughout the hours of daylight.

Philypnodon breviceps had two peaks of dry weight of stomach contents, one at midnight and the other at midday, indicating two peaks of feeding between the peak feeding times of G. vulgaris. The cycle of occurrence of empty stomachs followed closely the feeding cycle (see Fig. 42). However, there were always some P. breviceps with empty stomachs. Staples (1971, unpublished) reported diel periodicity in the feeding of age 1+ P. breviceps inhabiting a small lake: maximal feeding in summer, autumn and winter occurred in early afternoon, whilst in spring the diel pattern tended to be bimodal, with a lull in feeding before dawn and again during the middle of the day.

The diets of G. vulgaris and P. breviceps for all four-hourly samples combined are presented in Fig. 40. A comparison of the total diets using the Kendall rank correlation coefficient (see Table 38) indicates dissimilarity ($p > 0.05$), although ephemeropteran larvae formed the major part of the diet of both species. Terrestrial arthropods did not occur in P. breviceps stomachs, although they were taken quite regularly by G. vulgaris.

For each sample of G. vulgaris and P. breviceps over the 24-hour period, the percent occurrence and the points per fish for each of the major food items, together with the percent occurrence of the food items in the drift at the time of each sample, are presented in Fig. 43. It may be seen that although the same food items were eaten by the two fish species they were generally taken at different times during the 24-hour period. In a number of instances, the feeding of G. vulgaris on a particular item coincided with a period of abundance of the item in the drift. This occurred with the larvae of Deleatidium spp., C. humeralis, H. colonica and with terrestrial insects, and to a less extent with the larvae of Hydrobiosis sp. and Pycnocentrodes sp.: with the larvae of Deleatidium spp., C. humeralis and Hydropsyche sp., the closest relationship between occurrence in the drift and occurrence in G. vulgaris stomachs was found during the first half of the night. The positive correlation between the points allotted to terrestrial arthropods in G. vulgaris stomachs and the presence of terrestrial

arthropods in the drift occurred despite the fact that they were not found in the drift in large numbers at night, when G. vulgaris mainly feeds. Similarly, G. vulgaris was found to take more larvae of Pycnocentrodes sp. during daylight when the trichopteran was more abundant in the drift. However, G. vulgaris fed on the larvae of Nesameletus sp. mainly at night, even though Nesameletus sp. larvae were not common in the drift during the sampling period (n = 31) and occurred in approximately equal numbers throughout the 24-hour period.

The feeding of P. breviceps on its major food items was not positively associated with the occurrence of the items in the drift. For example, in the case of Deleatidium spp. larvae which were the major food items for both G. vulgaris and P. breviceps (see Fig. 40), and were also the dominant drifting group during the sampling period (n = 1,602), it was found that the occurrence of larvae in the stomachs of P. breviceps was not correlated with their occurrence in the drift, whereas their occurrence in the stomachs of G. vulgaris followed closely their abundance in the drift.

8. Feeding Mechanisms of the Fish Species in the River Glentui

To understand the feeding relationships of the fish in the River Glentui, information was required on the mechanisms of feeding in each species. This information was obtained from published work and from personal observations.

The dorsal brain pattern of each of the species was examined to obtain information on the relative importance of each sensory modality. The techniques used in the examinations were the same as those described in section 9.(2) of this chapter. The validity of the use of brain patterns to infer the feeding habits of fish is briefly discussed in section 9.(1). The brains of the fish species in the River were not compared, since phylogenetic differences would invalidate any comparisons of the relative importance of each sensory modality as indicated by the development of the appropriate part of the brain in each species. The brain patterns were used merely to indicate the important sensory modalities within each species.

Prepared transverse sections of the head of each species were stained with Heidenhains haematoxylin (Carleton, 1957) and examined for

the presence of taste buds.

(1) G. vulgaris

Benzie (1961, unpublished) reported adult G. vulgaris feeding in open water and occasionally going to the surface. Since this activity was more common on summer days than during wet or cold weather, it was inferred that there was a correlation between this behaviour and the presence of abundant flying insects. Eldon (1969), making observations in still-water aquaria (probably during the day), concluded that G. vulgaris is mainly a bottom feeder and noted that it spent "much time" swimming above the substrate with its "nose down on the gravel", although it would take food (live insects and dried preparations) from the water surface. Eldon (loc. cit.) reported that if no other species were present, G. vulgaris would rest on the bottom and become active when food was offered. In the present study, G. vulgaris was found to take food from all levels of the water column and off the bottom (see section 3. of this Chapter).

The presence of terrestrial insects in the stomachs of G. vulgaris in the River Glentui indicates that it takes some food items from the drift. It has been shown that in a number of instances the presence of certain food items in the stomach contents occurred during times of their abundance in the drift, particularly during the first half of the night. A number of workers (see e.g. Elliott, 1965) have shown that occurrence in the drift is related, at least partly, to the diel feeding patterns of benthic invertebrates, so that when animals move out onto the surface of rocks to feed, usually at night, they are more susceptible to becoming part of the drift. Ogilvie (pers. comm.) has observed the larvae of Deleatidium spp. feeding on the surface of rocks at night in the River Glentui. As pointed out by Elliott (1967c), the presence of animals both on the surface of stones and in the drift would increase their availability to fish such as trout which are primarily visual feeders. The occurrence of such items in the diet of fish may therefore reflect general activity cycles on the part of the prey animals, rather than occurrence in the drift. In either case the result is the same, i.e. an increase in the availability to fish such as G. vulgaris which are active in the water column at night (see section 3. of this Chapter).

FIGURE 44. Dorsal brain patterns of G. vulgaris, P. breviceps, S. trutta and A. dieffenbachii in fish of total lengths 84, 88, 110 and 250 mm respectively. The pineal body (which projects anteriorly above the forebrain) has been omitted for clarity.

Scale = 1 mm.

Key to letters:

at = acoustic tubercle.

c = cerebellum.

fb = forebrain.

fl = facial lobe of medulla oblongata.

m = medulla oblongata.

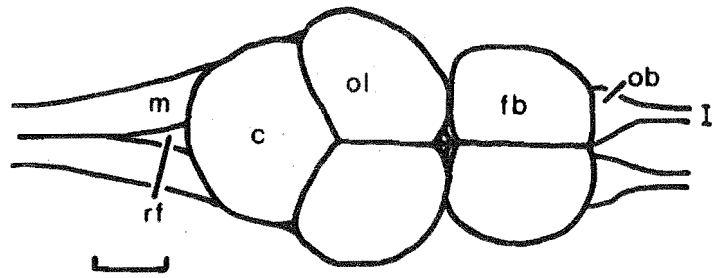
ob = olfactory bulb.

ol = optic lobe.

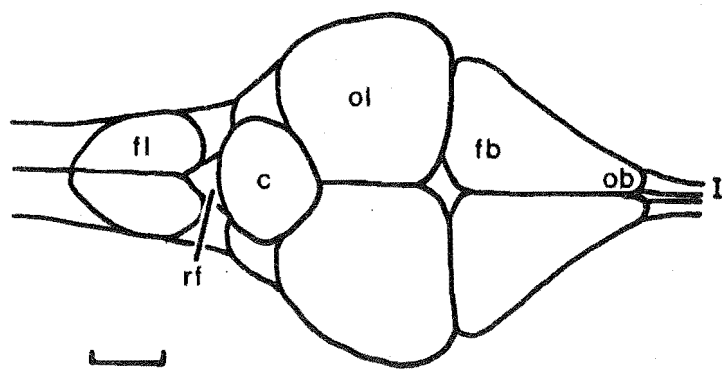
rf = rhomboid fossa.

I = olfactory nerve.

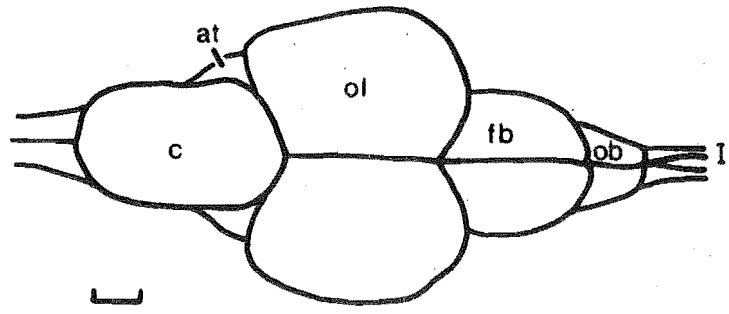
G.vulgaris



P.breviceps



S.trutta



A.dieffenbachii

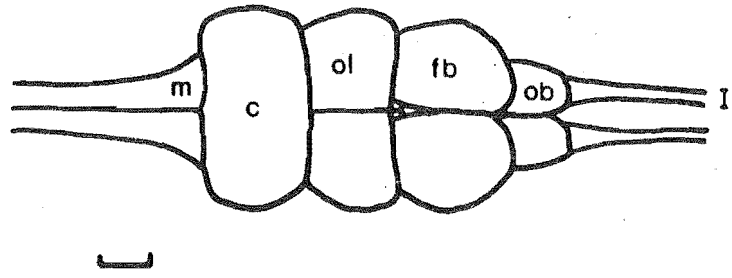


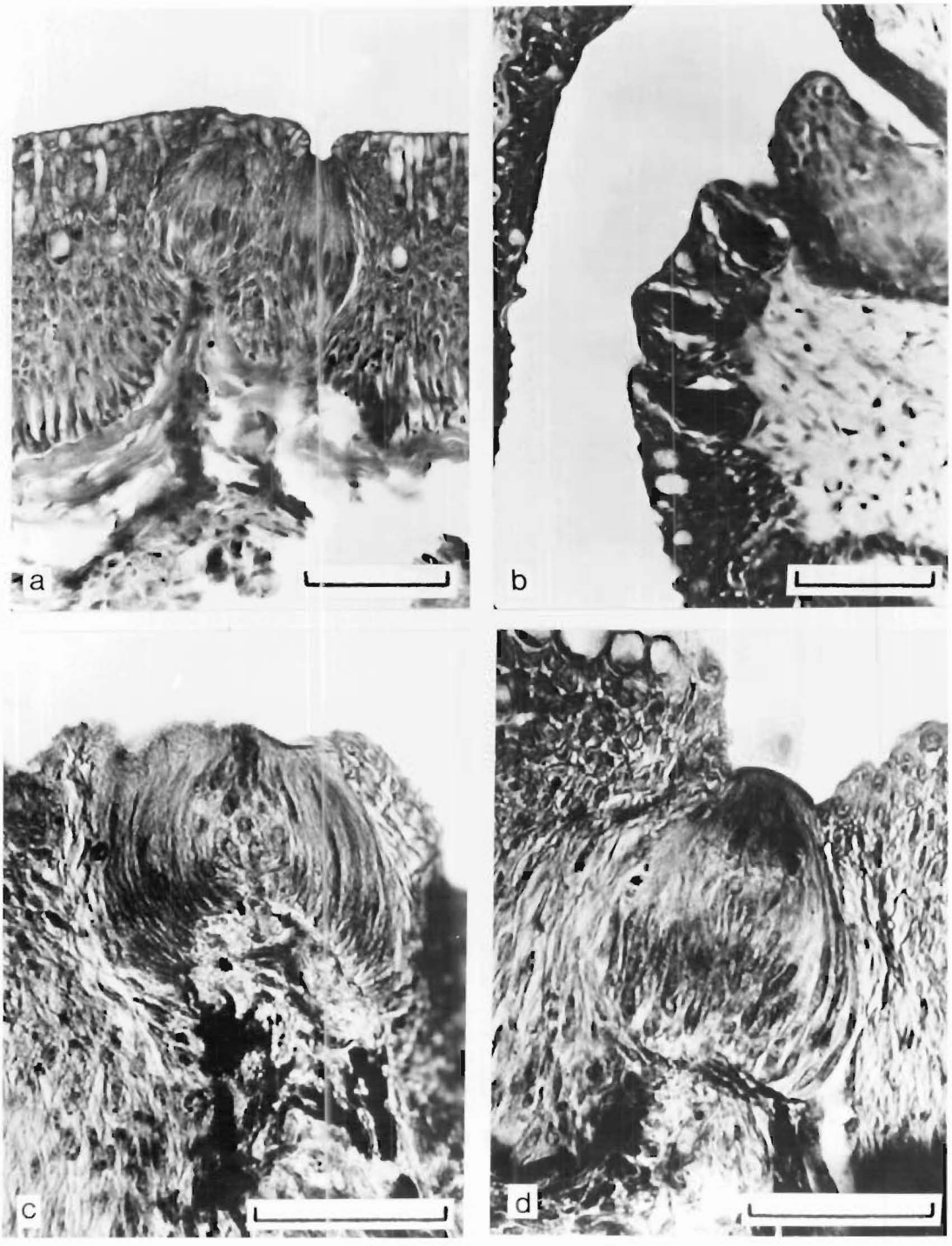
FIGURE 45. Taste buds of three of the fish species in the River Glentui. Scale = 0.05 mm.

a. *G. vulgaris* - two taste buds on the ventral surface of the head.

b. *S. trutta* - three taste buds within the lining of the mouth.

c & d. *P. breviceps* - single taste buds on the ventral surface of the head.

(Photographs ; a and b - J. L. Burnip; c and d - T. K. Crosby.)


a
b
c
d

That vision plays an important role in the life of G. vulgaris is indicated by the size of the optic lobes of the brain (see Fig. 44). However, the relative size of the optic lobes decreases with increasing fish size and is associated with a corresponding increase in the size of the forebrain (see section 9.(3) of this Chapter), perhaps indicating an increase in the importance of olfaction in larger fish. Numerous small taste buds (see Fig. 45) are present on the dorsal and ventral surfaces of the head, on the lips and within the mouth, and G. vulgaris has been observed in laboratory aquaria to reject inedible particles which it has taken into its mouth. However, the degree to which rejection occurs in nature probably depends on feeding conditions.

In New Zealand, brown trout, which are essentially visual feeders (see later) and also possess taste buds in the mouth (see Fig. 45), tend to contain more inedible objects in their stomachs when taken from streams than when taken from lakes (Clark, pers. comm.). Van Someren (1950a, quoted by Carlander, 1969) recorded 60 - 80% occurrence of inedible items such as stones in the stomachs of S. trutta taken in streams. Lake fish and those inhabiting the more quiet stretches of rivers and streams probably have more time to taste and reject objects than do fish taking items out of the stream drift. In the latter situation, the prey organisms are moving downstream past the fish so that capture must be rapid, otherwise the food item is lost. Under such circumstances it might be expected that inedible items would occasionally be taken into the stomach. As indicated by Lindstrom (1955) and Nilsson (1957), movement is probably the most important stimulus to drift feeders, so that any object moving downstream is a potential food item. In the River Glentui, 17.8% of G. vulgaris examined (n = 924) contained gravel in their stomachs, whereas only 2.8% of P. breviceps examined (n = 430) contained gravel. Furthermore, the occurrence of gravel in G. vulgaris stomachs increased with increasing fish size (see Table 41). The gravel, generally of the size range 1 - 2 mm, was larger than the particles used by the larvae of Pycnocentria sp. and Pycnocentrodes sp. to construct their cases and was therefore not derived from the break-down of trichopteran cases. Since stony trichopteran larval cases (< 10 mm long) do not accumulate in fish stomachs, it may be assumed

TABLE 41. Percent occurrence of inedible items (gravel) in the stomachs of G. vulgaris in different length groups. (n = sample size).

Length (mm)	n	% occurrence of gravel	Length (mm)	n	% occurrence of gravel
<29	60	0	70 - 79	120	15.8
30 - 39	17	0	80 - 89	154	25.3
40 - 49	51	3.9	90 - 99	89	27.0
50 - 59	213	8.9	100 - 109	59	40.7
60 - 69	147	15.0	>110	14	42.9

that other inedible material is egested, so that gravel does not accumulate in G. vulgaris stomachs. The increase in occurrence of gravel in fish of increasing size most probably reflects feeding position in the stream. Larger fish were found to occupy more rapid parts of riffles than smaller fish (see Chapter VII) and therefore would be expected to take more inedible objects if they fed on drift. Small G. vulgaris (< 40 mm) did not contain gravel in their stomachs; however, this probably reflects their small gape, rather than their occupancy of the more quiet parts of the River. It is considered that the difference in the occurrence of gravel in G. vulgaris and P. breviceps stomachs reflects a difference in the feeding habits of the two species, with G. vulgaris being more of a drift-feeder than P. breviceps.

The shape of G. vulgaris is a further indication of its feeding habits. The round cross-section and streamlined shape, as in salmon and trout, are indicative of a fish which regularly swims in fast running water (Hubbs, 1941; Hynes, 1970a).

To summarize, G. vulgaris is essentially a visual feeder, with olfaction perhaps playing a more important role in large fish. Although numerous small taste buds are present, the sense of taste is not well developed. Field and laboratory data indicate that food is taken from the drift and also from the substrate at a time when many of the prey organisms are more accessible to fish swimming in the water column.

(2) P. breviceps

Hopkins (1970), working in small streams, mentioned that P. breviceps searches for food on the bottom. Staples (1971, unpublished), working on a lake population, found that most of the food items eaten were characteristically weed and bottom-dwelling species. In the present study, there was no correlation between the occurrence of food items in the drift and in the stomachs of P. breviceps during a 24-hour period. Potamopyrgus antipodarum, which did not occur in the drift, was found occasionally in P. breviceps stomachs, whereas it did not form part of the diet of G. vulgaris. Out of 430 P. breviceps stomachs examined, only two contained terrestrial insects. That P. breviceps is a bottom-dweller is indicated by its shape and the position of its eyes (see Woods, 1963:42).

Crumpton (1968, unpublished) indicated that vision is important in the feeding of P. breviceps. She found that when small swimming crustaceans were present, P. breviceps would ingest them with a gulping movement after swimming after them, or after the organism had swum into its mouth. Larger wormlike organisms were always actively pursued. Non-food particles (carmine) were not ingested by starved fish during trials lasting for one hour.

The size of the optic lobes of the brain (see Fig. 44) indicates that vision plays an important role in the life of P. breviceps. Sections of the head of P. breviceps reveal small taste buds within the mouth and on the lips, and large taste buds on the ventral surface of the head (see Fig. 45) which are much more elaborate than the smaller taste buds and resemble the taste buds found on the barbels of the sturgeon, Acipenser fulvescens (see Hara, 1971). The presence of such well developed taste receptors in the skin is reflected in the development of the facial lobes of the myelencephalon (see Fig. 44). In many species of fish, these lobes fuse in the midline to form the tuberculum impar (Miller and Evans, 1965). Since the work of Herrick (1902, 1903), a number of workers have demonstrated a relationship between the development of the facial lobes and "skin tasting" in a number of taxonomic groups (see e.g. Evans H.M., 1931, 1932, 1935, 1940; Bhimachar, 1935, 1937; Sato, 1941; Mookerjee et al,

1950; Evans H. E., 1952; Miller and Evans, 1965; Davis and Miller, 1967).

Philypnodon breviceps may, therefore, be regarded as a bottom feeder in which vision and taste play important roles in the location and capture of food.

(3) S. trutta

The role of vision in the feeding of S. trutta is well established (see Chapman, 1966; Frost and Brown, 1967), though olfaction may be important in poor light (Wunder, 1927, quoted by Kleerekoper, 1969). The importance of vision is reflected in the large size of the optic lobes of the brain (see Fig. 44 and Parker and Haswell, 1947:250). Taste buds are present in the mouth (see Fig. 45), but as discussed previously, their effectiveness probably depends on feeding conditions. However, McCormack (1962) observed S. trutta in a small stream taking water-borne animals and then sometimes rejecting them, indicating that palatability of food organisms may be quite important in determining the diet.

Although S. trutta takes food from the bottom (Horton, 1961; Frost and Brown, 1967; Tusa, 1968, 1969; Mann and Orr, 1969), it appears to obtain the greater proportion of its food from the drift (Muller, 1954; Nilsson, 1957; McCormack, 1962; Thomas, 1962; Elliott, 1967c, 1970; Frost and Brown, 1967; Chaston, 1968c; Tusa, 1968, 1969; Bishop and Hynes, 1969; Jenkins, 1969; Mann and Orr, 1969).

(4) Anguilla spp.

As pointed out by Sinha and Jones (1967) and Hopkins (1970), Anguilla spp. are essentially bottom-feeders. Their olfactory acuity is particularly high (Kleerekoper, 1969) and their olfactory organ is well developed (Hasler, 1957; Hara, 1971). This is reflected in the development of the forebrain (see Fig. 44) which, apart from a number of other functions (see section 9. of this Chapter), is responsible for the reception, elaboration and conduction of olfactory impulses (Lagler, Bardach and Miller, 1962). Numerous small taste buds, similar to those found in G. vulgaris and S. trutta (see Fig. 45), were found in the mouth, on the lips and in the skin of the head of A. dieffenbachii.

Anguilla australis was not examined for the presence of taste buds. The small size of the eyes in Anguilla spp. indicates a minor role for vision and this is reflected in the relatively small size of the optic lobes of the brain.

In the River Glentui, eels were found to be more active at night, when they normally feed (Cairns, 1942), than during the day. Feeding behaviour is probably similar to that described by Bardach, Winn and Menzel (1959) for the nocturnal moray eels, Gymnothorax moringa and Gymnothorax victinus. Their experiments indicated that olfaction is used in the location of food and that, once approached, taste stimuli elicit grasping. They suggested that tactile receptors possibly play a subsidiary role in the latter response. The success of baited traps in capturing Anguilla spp. in New Zealand (Cairns, loc. cit.; Burnet, 1952) attests to the efficiency of food location by means of olfaction in these species.

The feeding relationships of the fish species in the River Glentui are discussed in Chapter VII, after a consideration of the spatial distribution of the fish within the River.

9. The Relationship Between the Dorsal Brain Pattern and the Ecology of the New Zealand Galaxiidae

(1) Introduction

The teleost brain is primarily organized on the reflex level, so that it reflects the correlation between sensory adaptation and principle modes of activity more clearly than the brain of higher vertebrates (Miller and Evans, 1965; Davis and Miller, 1967; Tuge et al, 1970). It is therefore suitable for correlative studies of sense organs, brain pattern and behaviour. However, the various parts of the brain also have higher level functions (see review by Aronson, 1963). For example, evidence suggests that the forebrain has major functions other than olfaction (Meader, 1939; Maliukina and Flerova, 1960). Aronson and Kaplan (1968) indicated its importance in the mediation of learning processes and pointed out that it may also have a special relation to the visual system in some groups of fish in which vision is the dominant sensory modality. The evidence for and against the localization of learning and memory processes in the forebrain has been

recently reviewed by Gleitman and Rozin (1971) who summarized the matter by quoting Janzen (1933) who described the forebrainless fish as "lacking in initiative." Despite higher level functions, it is possible to recognize the predominant sensory modalities and infer with accuracy the feeding behaviour, and in some instances the habitat, of a fish by an examination of its external brain morphology.

Evans (1931, 1932, 1935, 1940) examined the relationship between the brain pattern and ecology of a number of British fish. He divided the cyprinids into three groups depending on the morphology of the hind brain. The members of each group had similar feeding habits and possessed certain common characteristics. The first group contained species whose vagal lobes were large: these fish could extract nourishment from mud. The second group had small facial and vagal lobes and were primarily visual feeders, whilst the third group possessed a large facial lobe associated with the presence of sensory barbels. Bhimachar (1935), Sato (1941) and Evans (1952) found similar groupings in Indian, Japanese and American cyprinids. Also, Bhimachar (1937) found that cyprinodonts, which are generally visual feeders in which the gustatory system is of secondary importance, had small facial and vagal lobes.

Mookerjee, Ganguly and Mookherji (1950) studied the brains of 25 species in 13 families and classified them into three groups according to their brain structure and feeding habits. Fish in the first group possessed well developed facial lobes and less prominent optic lobes and tracts; they fed mainly by taste on the bottom or in midwater. Fish in the second group fed both on the surface and at the bottom, using both vision and taste; they possessed well developed facial lobes or vagal lobes or both and had prominent optic lobes. The fish in the third group were surface feeders relying on vision: they had poorly developed facial and vagal lobes, but structures associated with vision were well developed.

Miller and Evans (1965) examined the brains of 46 species in 13 genera of catostomids, all of which possessed prominent facial and vagal lobes. Some fish possessed relatively larger vagal lobes, whilst others, particularly those with large papillose lips, possessed relatively larger facial lobes. Sections of the sensory epithelium revealed that

the latter group had large numbers of taste buds on the lips and few on the palatal organ, while the condition was reversed in the former group. Davis and Miller (1967) found a close correlation between the brain patterns in minnows of the genus Hybopsis and their feeding habits and habitat. Variability in brain lobes was found to be greatest in species inhabiting the most variable habitats.

Within a species, the brain pattern may be used to indicate predominant sensory modalities in different size groups. For example, Uchihashi and Yamaguchi (1955) recorded size-related changes in the morphology of the brain of Mylio macrocephalus and found that the proportional enlargement of the forebrain was correlated with the development of nocturnal behaviour. Also, Ogawa (1968) reported that in the horse mackerel, Trachurus clupeiodes (Whitley, 1968), there was a close correlation between changes in behaviour and morphological changes in some brain components, especially the optic lobes, cerebellum and forebrain. Similarly, Marinesco (1968b) found that in Protherorhinus marmoratus and Benthophilus stellatus (Gobiidae) the same three components were the most variable brain vesicles. In the Cyprinidae, Schmidt (1967, 1968) found intraspecific changes in brain morphology and development of the eyes which were related to the ecology of the fish. As pointed out by Miller and Evans (1965), such changes are probably quite common in fish brains, particularly in species which gradually develop specialized feeding habits as adults after feeding in a generalized manner at earlier stages.

In the present investigation, the dorsal brain pattern of G. vulgaris in different size-groups was examined in order to establish the dominant sensory modalities at different stages of the life cycle. The dorsal brain patterns in different size-groups of G. vulgaris were then compared with the brain patterns of juvenile and adult fish of two other species of Galaxiidae, viz. G. maculatus and N. burrowsius, whose juvenile and adult ecology is reasonably well understood. The adult brain patterns of the other New Zealand Galaxiidae were then examined in an attempt to elucidate the ecology of the lesser known species.

A detailed description of the galaxiid brain and cranial nerves

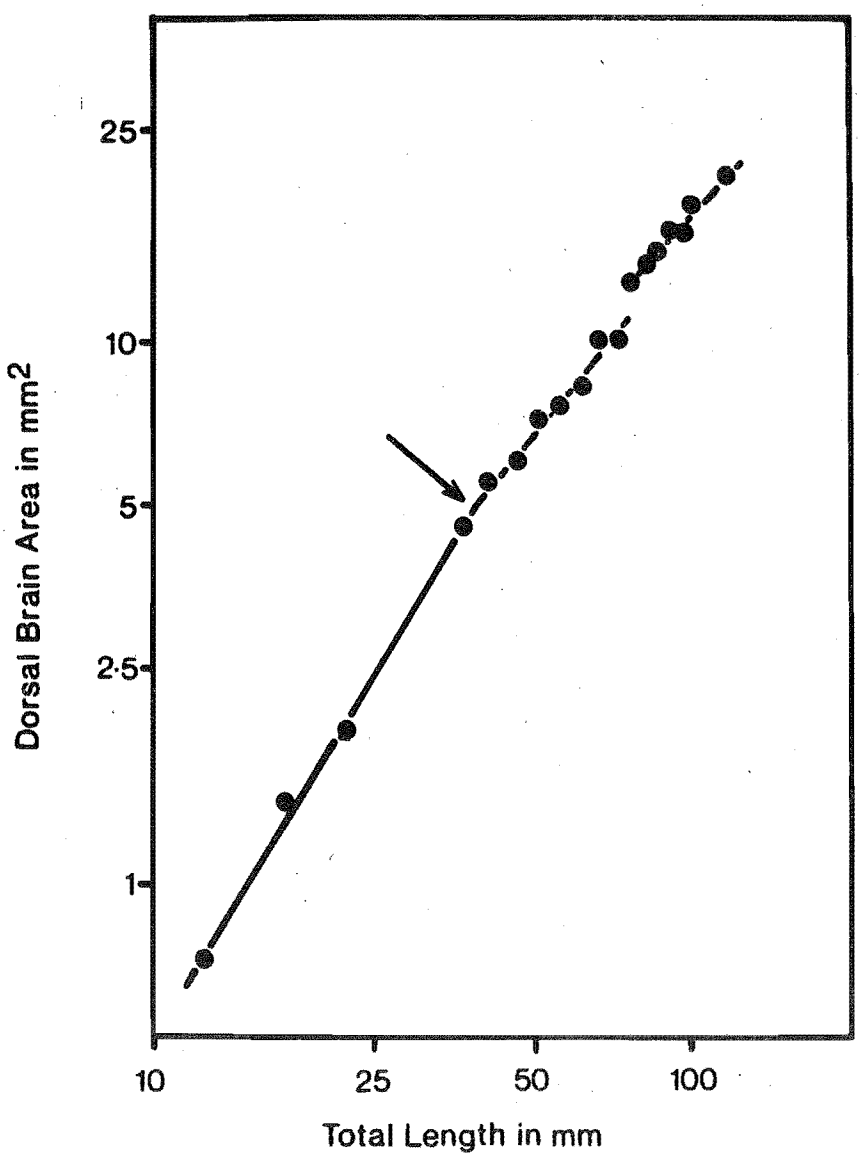
has been given by McKenzie (1935, unpublished) who described the nervous system of Galaxias attenuatus (= G. maculatus) and indicated its overall similarity to the brain of Salmo. In the present study, preliminary observations indicated that the medulla of galaxiids is, externally, relatively simple, as in salmonids (see Fig. 44; Parker and Haswell, 1947: 250; Tuge et al, 1970:46), and does not possess externally visible swellings (vagal and facial lobes) which mark the primary receptive nuclei of gustation in other taxonomic groups, e.g. cyprinids and catostomids. Thus, although the gustatory sense may vary in importance in different-sized individuals of G. vulgaris or between the adults of different species of Galaxiidae, the differences cannot be assessed by an examination of the external morphology of the hind-brain. Comparisons of the brains of different individuals of G. vulgaris and different species of Galaxiidae were therefore confined to an examination of the absolute and relative sizes of the cerebellum, forebrain and optic lobes. Although taste buds are present in G. vulgaris (see Fig. 45 and section 8.(1) of this Chapter), the gustatory sense does not appear to play a major role in this species.

(2) Methods

Each brain was inspected after picking away the roof of the cranium with fine forceps. The soft tissue immediately beneath the roof of the cranium was removed, followed by the pia mater which closely adheres to the brain surface and whose position is indicated by the occurrence of chromatophores on the surface of the brain. Each brain was examined beneath a dissecting microscope fitted with a grid eye-piece. Dorsal brain patterns were drawn onto a standard-grid drawing sheet, the scale of which was calibrated separately for each magnification used. The surface areas of the cerebellum, optic lobes and forebrain were measured from the drawings using a planimeter. Although surface areas do not reflect exact brain lobe dimensions, they provide indices with which the brain lobes of individuals of the same species or of closely-related species may be compared.

The source localities for the specimens are given in Appendix 2.

FIGURE 46. Relationship between total fish length and dorsal brain area in G. vulgaris. Both variables are plotted logarithmically. Points are mean values for fish in 5 mm length classes. Number of fish examined = 75; length range of fish examined = 11 - 122 mm. For further explanation see text of section 9.(3).


25
10
5
2·5
1
Dorsal Brain Area in mm2
10
25
50
100
Total Length in mm

(3) Size-related changes in the relative proportions of the forebrain, optic lobes and cerebellum in G. vulgaris

In estimating the growth of the brain of G. vulgaris, only the optic lobes, cerebellum and forebrain, i.e. the components which comprise most of the dorsal brain area (see Fig. 44), were considered. The areas of these three components were combined in order to examine the increase in size of the brain (i.e. dorsal brain area) with increase in fish size. The relationship between the dorsal brain area and total fish length in 75 G. vulgaris is presented in Fig. 46. Both variables were transformed to logarithms and, to clarify any changes in relative growth between dorsal brain area and fish length, data were grouped into 5 mm length-classes and mean values for each class were plotted. It may be seen that there are three distinct phases in the relationship between the two variables. The boundary between the first and second phases is indicated by an arrow (see Fig. 46) and corresponds to the length at which juvenile fish leave the quiet stretches of the River for the adult riffle habitat, a period which is associated with a number of physiological adjustments (see Chapter V, section 7.). Also, the change from the juvenile to adult ratio of standard length to head length is normally complete by this time (Benzie, 1961 unpublished). The second and third phases are separated from each other by a clear hiatus in values. Such changes in size relationships are often found in arthropods before and after critical moults (see Teissier, 1960). However, the stimulus for the marked change in G. vulgaris is not clear, although it occurs in the length range at which the growth rates of males and females begin to differ (see Chapter III).

Thus, there are changes in the relationship between fish total length and dorsal brain area which occur at total lengths of approximately 40 and 75 mm. Having distinguished three phases, the coefficients of allometry for each phase (see Simpson, Roe and Lewontin, 1960; Teissier, loc. cit.), i.e. the slopes of the regression lines, were computed from total data (i.e. not mean values of 5 mm length classes which were used to distinguish the three phases) and are presented in Table 42, together with the coefficients of allometry in each phase for fish total length and the dorsal areas of the forebrain, optic lobes and cerebellum.

FIGURE 47. Changes in the relative proportions of the forebrain, optic lobes and cerebellum with increase in length of G. vulgaris. Each component is represented as a percentage of the total dorsal brain area (viz. the dorsal surface areas of the forebrain, optic lobes and cerebellum combined). Number of fish examined = 75; length range of fish examined = 11 - 122 mm.

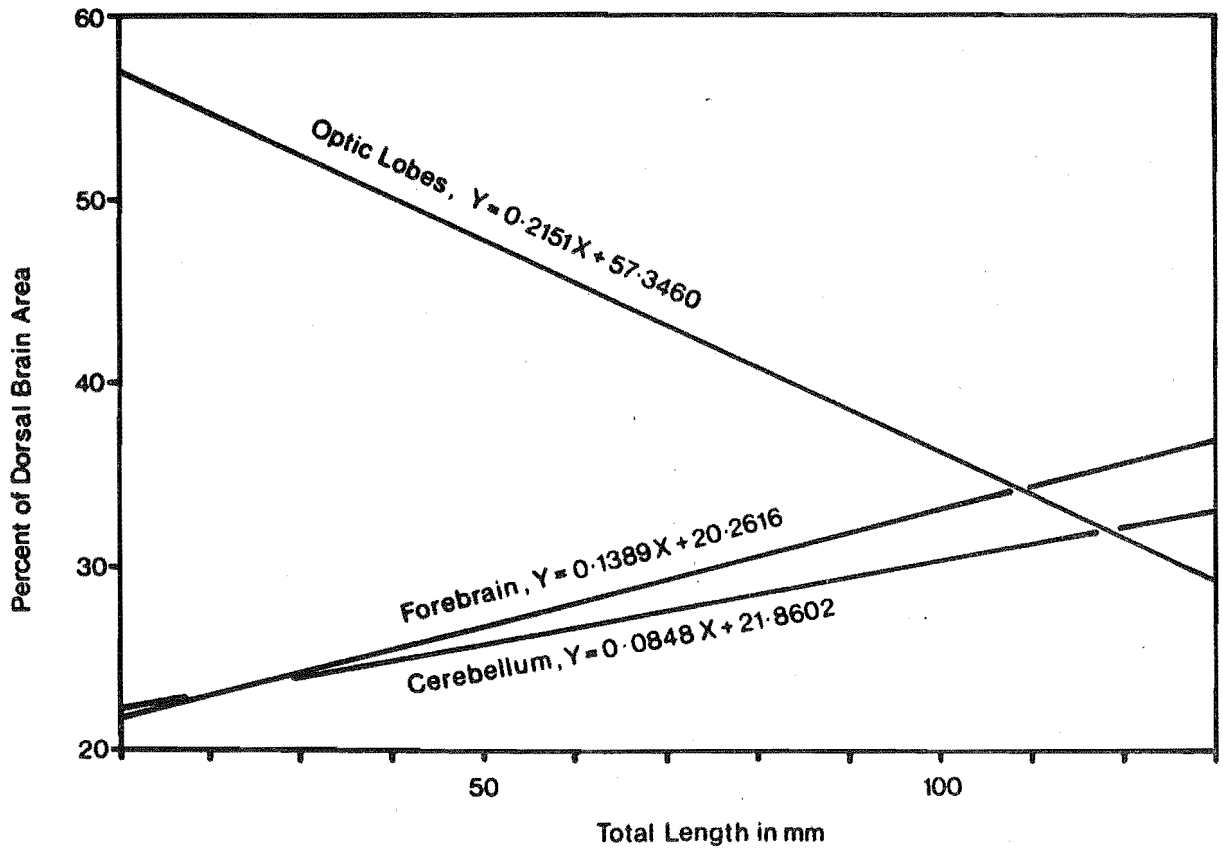

60
50
40
30
20
Percent of Dorsal Brain Area
Optic Lobes, Y = 0·2151X + 57·3460
Forebrain, Y = 0·1389X + 20·2616
Cerebellum, Y = 0·0848X + 21·8602
50
100
Total Length in mm

FIGURE 48. Dorsal brain patterns of a generalized juvenile galaxiid (based on the dorsal brain patterns of juvenile G. maculatus, G. fasciatus, G. divergens, G. brevipinnis, G. vulgaris and N. burrowsius) and adults of G. maculatus (TL = 82 mm), G. vulgaris (TL = 85 mm) and N. burrowsius (TL = 84 mm). In each instance, the pineal body has been omitted and, to facilitate comparisons, the brains are not drawn to scale. See text of section 9.(4) for explanation.

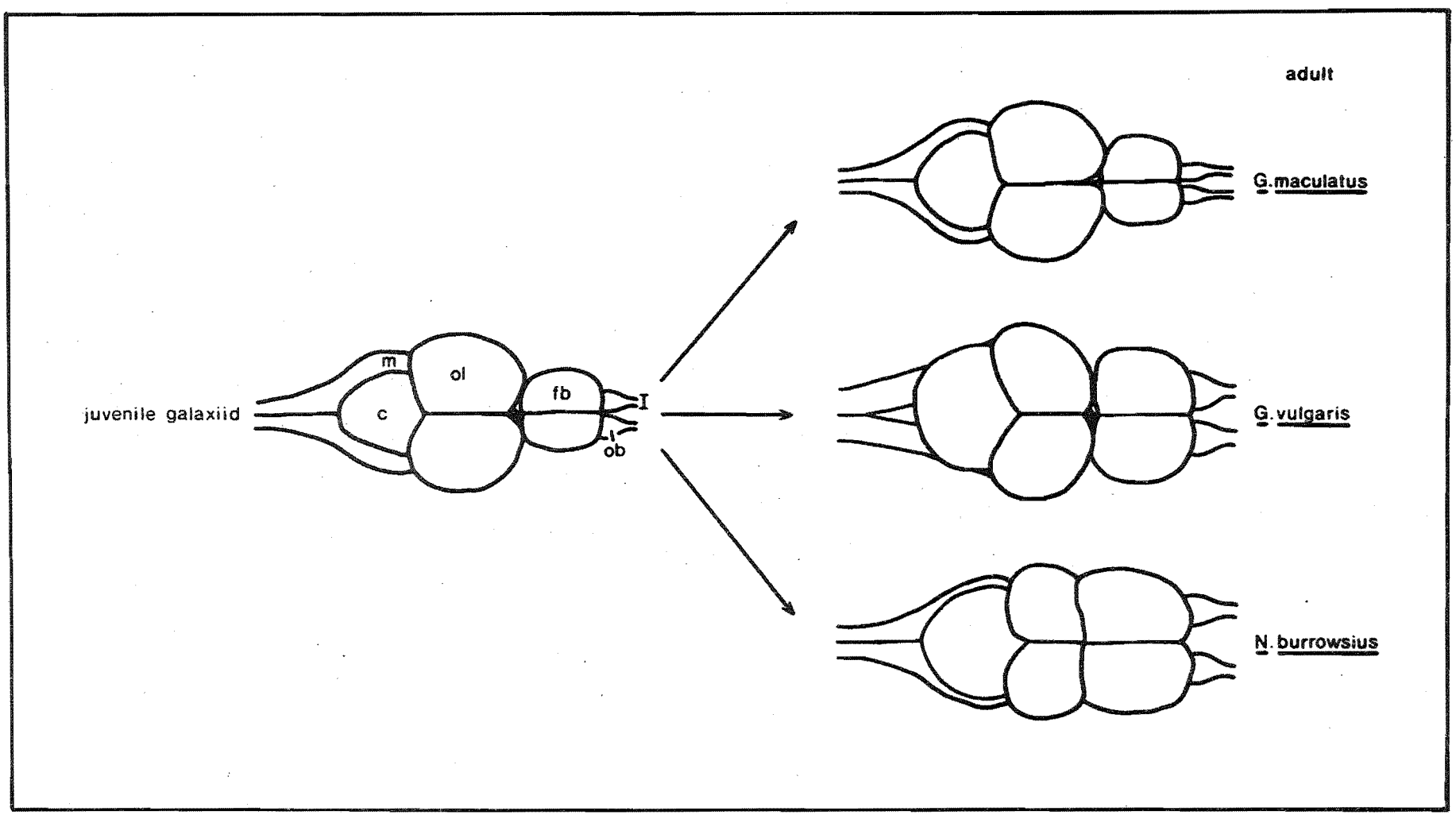

adult
juvenile galaxiid
m
ol
c
fb
I
ob
G.maculatus
G.vulgaris
N.burrowsius

TABLE 42. Allometric coefficients for the relationships between total fish length and dorsal surface areas of the whole brain (i.e. forebrain, optic lobes and cerebellum combined), forebrain, optic lobes and cerebellum in the three phases of growth indicated in Fig. 46 (n = sample size).

Phase	TL (mm) range	n	Total brain	Forebrain	Optic lobes	Cerebellum
1	< 40	11	1.2899	1.5155	1.2437	1.3563
2	40 - 75	35	1.2598	1.4942	1.0805	1.3680
3	> 75	29	1.1519	1.5653***	0.7028*	1.0255

* significant deviation from 1 at the 0.05% probability level
*** significant deviation from 1 at the 0.001% probability level

It may be seen that for each phase, the relationship between fish length and dorsal brain area is isometric, with none of the values being significantly different from unity. This indicates that fish length and dorsal brain area are growing in parallel (Teissier, loc. cit.). The same situation also holds for the relationship between total fish length and the dorsal surface areas of the forebrain, optic lobes and cerebellum, with the exception of the forebrain and optic lobes in fish longer than 75 mm. In this third phase, the relationships between fish length and the dorsal surface areas of the forebrain and optic lobes are allometric. In the case of the forebrain, there is positive allometry, i.e. the increase in size of the forebrain is more rapid than the increase in fish length, whilst in the case of the optic lobes, there is negative allometry, i.e. the increase in size of the optic lobes is less rapid than the increase in fish length. Such allometric growth of brain lobes in fish has also been recorded by Geiger (1956a, b, quoted by Davis and Miller, 1967) and Schwarz et al (1968). The optic lobes are therefore relatively larger in small fish than in large fish, whilst the situation is reversed with the forebrain (see Fig. 47 and Fig. 48).

As pointed out by Uchihashi and Yamaguchi (1955) for M. macrocephalus (see section 9.(1) of this Chapter), the proportional

enlargement of the forebrain in G. vulgaris is probably correlated with the development of nocturnal behaviour and the cryptic way of life of the adult fish. Although juvenile G. vulgaris soon become predominantly nocturnal (see section 3.(2) of this Chapter), they continue their open water existence in the quiet stretches of the River until they reach a total length of about 40 mm, when they move into the riffle habitat. Within the riffles, it was found that the largest fish tended to occur in the most turbulent areas (see section 1.(1) in Chapter VII). There is therefore a correlation between the movement from the quiet stretches of the River to the most turbulent parts of the riffles and the proportional enlargement of the forebrain and reduction of the optic lobes. Vision appears to play an important role throughout the life of G. vulgaris and is certainly the dominant sensory modality in juvenile fish. However, as the fish increase in size, the development of the forebrain indicates that perhaps olfaction plays a more important role in the ecology of the adult fish than in the juveniles.

In Fig. 48 it may be seen that the cerebellum, whose major function is the control of movement (Lagler, Bardach and Miller, 1962; Aronson, 1963), is proportionally larger in large fish than in small fish. Again this probably reflects the change from the quiet-water existence of the juveniles to the riffle habitat of the adults. In the latter situation, with high water velocities, control of movement would need to be more stringent than in quieter, gently-flowing waters.

(4) A comparison of the dorsal brain patterns of juvenile and adult G. vulgaris, G. maculatus and N. burrowsius.

Juveniles of G. vulgaris, G. maculatus and N. burrowsius are free-swimming, shoaling, non-cryptic and active during daylight (see Appendix 1; Chapter IV; Benzie, 1961 unpublished, 1968d; McDowall, 1968a, 1970). As adults, G. maculatus retain the open-water behaviour of the juveniles and are active during daylight: under certain conditions they may also from shoals (Benzie, 1961 unpublished; Eldon, 1969; McDowall, 1970). Although found in diverse habitat types, they normally occur in stable lowland streams in gently flowing water (McDowall, 1970). Adult G. vulgaris inhabit stream riffles (see Chapter V) and are essentially nocturnal (see section 3.(2) of this Chapter). Neochanna burrowsius

TABLE 43. Proportions of the dorsal brain area (as percentages of the total dorsal brain area) occupied by the forebrain, optic lobes and cerebellum in the New Zealand Galaxiidae. Species are arranged in descending order of eye size, as indicated by the ratio of horizontal fleshy eye diameter (DE) and head length (HL). (n = sample size; TL range = the range of total lengths of the fish examined).

		Adults					Juveniles			
Species	DE/HL*	n	TL range (mm)	forebrain	optic lobes	cerebellum	n	TL range (mm)	forebrain	optic lobes	cerebellum
G. gracilis	24.3	7	35–53+	19–23	52–63	16–26					
G. maculatus	21.8	14	64–133	25–31	45–57	15–24	17	45–62	20–28	52–61	16–24
G. fasciatus	20.2	5	85–209	29–38	41–49	19–28	5	44–46	16–32	49–68	13–19
G. postvectis	19.9	3	50–207	24–29	45–52	24–25					
G. divergens	18.2	3	59–69	25–29	44–49	25–27	4	20–33	23–26	49–54	23–27
G. brevipinnis	17.8	4	72–163	27–39	36–45	17–32	8	50–56	19–28	41–58	16–31
G. argenteus	17.7	3	125–250	31–32	38–45	23–31					
G. vulgaris	17.6	64	48–122	25–37	34–51	25–37	11	10–41	18–28	48–58	18–29
G. paucispondylus	15.0	5	62–69	24–28	39–46	29–30					
G. prognathus	14.1	5	63–74	31–36	33–41	27–32					
N. diversus	13.0	5	44–118	32–42	31–36	26–32					
N. burrowsius	12.5	34	54–155	29–48	27–39	21–35	5	26–39	24–33	46–49	21–27
N. apoda	8.3	4	62–130	36–37	32–36	27–31					

* data from McDowall (1970), figures are percentages of the denominator of the ratio

\+ G. gracilis is a small fish, the maximum recorded size being only 62.5 mm (McDowall, loc. cit.)

adults are also nocturnal; they are capable of burrowing into mud and are normally found in still or sluggish man-made or man-modified habitats, although their natural habitat appears to be swamps and other unstable bodies of water which periodically dry up (see Appendix 1).

The juvenile and adult brain patterns of the three species (see Fig. 48) reflect the similarities and differences between the ecology of the two size groups. In all three species, the optic lobes of the juveniles are relatively large, whilst the forebrain is relatively small. The same condition persists in adult G. maculatus, which retain the open-water habit of the juveniles (see also Table 43). However, in adult G. vulgaris the forebrain becomes relatively larger with increase in fish length (see also previous section and Fig. 47), whilst in the burrowing adult N. burrowsius the trend is carried still further with, in some instances, the forebrain accounting for up to 45% of the total dorsal brain area (see also Table 43).

In N. burrowsius and G. maculatus the relative size of the cerebellum is similar in juveniles and adults, whereas in G. vulgaris the cerebellum is relatively larger in adults than in juveniles. As pointed out in the previous section, the change in the relative size of the cerebellum in G. vulgaris is probably associated with the change from quiet to more rapid-flowing waters. In N. burrowsius, the adults occupy the same habitat as the juveniles. Although juvenile G. maculatus occur in the sea before migrating to the adult habitat (see Chapter IV, section 1.), it appears, from an examination of the relative sizes of the cerebellum in juveniles and adults, that the two habitats make similar demands on the motor coordination centres of the cerebellum.

(5) A comparison of the dorsal brain patterns of the New Zealand Galaxiidae

The proportions of the dorsal brain area occupied by the forebrain, optic lobes and cerebellum in each of the New Zealand Galaxiidae are presented in Table 43. Juveniles of six species (including G. vulgaris, G. maculatus and N. burrowsius) were examined and in all instances, the relative proportions of the various components of the brain were similar. All have large optic lobes (41 - 68% of the

dorsal brain area), a small forebrain (16 - 33%) and a relatively small cerebellum (13 - 29%). In the previous section, the free-swimming, open-water habit of the juveniles of G. vulgaris, G. maculatus and N. burrowsius was described. It would appear from the similarity in dorsal brain patterns that G. divergens and the migratory G. fasciatus and G. brevipinnis have similar habits. In the case of G. divergens this has been confirmed by Hopkins (1971a) who observed juveniles swimming in mid-water.

Adult Galaxiidae show great interspecific diversity in the relative proportions of the various brain components. As might be expected there is a marked positive correlation between the size of the eye and the relative size of the optic lobes, with a negative correlation between eye size and the relative size of the forebrain. Vision is important in the feeding of galaxiids (see section 8.(1) of this Chapter), although olfaction probably plays a significant role in the more nocturnal species. Galaxias maculatus, with its large optic lobes and small forebrain, is open-living and active during the day, whilst G. vulgaris and the mudfish, viz. N. diversus, N. burrowsius and N. apoda, are essentially nocturnal (see section 3.(2) of this Chapter; Appendix 1; Eldon, 1969). A relatively large forebrain, e.g. as in G. argenteus and G. prognathus, may therefore be indicative of predominantly nocturnal behaviour. Eldon (loc. cit.) has reported that in aquaria, G. argenteus normally only leaves its cover at night to feed, although it may sometimes be seen at the surface of quiet, deep swamp pools during the day. On the other hand, a relatively small forebrain and large optic lobes may be taken as indicative of a more open-living existence. For example, G. fasciatus (see Table 43) has been observed to form shoals in the pools of small streams (Eldon, loc. cit.). Since G. vulgaris adults, which inhabit riffles, have a relatively larger cerebellum than G. vulgaris juveniles, which inhabit quiet reaches, it might be expected that adults of species inhabiting fast-flowing streams and rivers would have a relatively larger cerebellum than those inhabiting lakes, or slow-flowing waters. In certain species this is found to be the case: G. gracilis and G. maculatus, each with a relatively small cerebellum,

are found in lakes (G. gracilis and G. maculatus) and slow-flowing rivers and streams (G. maculatus), whereas G. paucispondylus and G. prognathus, with a relatively large cerebellum, are found in rapid-flowing waters. In other species the relationship is not so clear. The mudfish, which inhabit sluggish waters, have a relatively large cerebellum. However, this may reflect their burrowing ability.

A number of workers (e.g. Svetovidov, 1953; Kirka, 1963; Marinesco, 1968a) have attempted to use brain morphology as a taxonomic character. However, ecological factors have been found to have such a profound influence on the relative proportions of the brain lobes that, although brain morphology may reveal higher phylogenetic relationships, it cannot be used with accuracy to differentiate species within the same genus. Similarly, within the New Zealand members of the family Galaxiidae, although there is an overall similarity in brain patterns, there is ecologically-related variation within and between species, such that any two species may have similar brain patterns depending on their ecology at different stages of their life history. For example, both adult G. maculatus and juvenile G. vulgaris are open-living and free-swimming and are found in gently-flowing water, and consequently have similar brain patterns. For the Galaxiidae, as pointed out by Miller and Evans (1965) for catostomids and by Davis and Miller (1967) for minnows of the genus Hybopsis, the principle value of comparative brain morphology lies in providing a basis for making inferences about the life history, particularly the habitat preferences and feeding behaviour, of little known species, rather than as a taxonomic tool for differentiating closely related species.

Chapter VII

RELATIONSHIPS BETWEEN GALAXIAS VULGARIS AND THE OTHER FISH SPECIES IN THE RIVER GLENTUI

In this Chapter, interspecific relationships, including competitive interactions, of the fish species in the River Glentui are considered. To avoid ambiguity, a working definition of interspecific competition is required. Crombie (1947), Birch (1957), Milne (1961), De Bach and Sudby (1963) and Miller (1967) have reviewed the literature on interspecific competition, a concept which has been the subject of great discussion, both semantic and otherwise, since the work of Darwin (1859). Lagler (1944), Larkin (1956), Le Cren (1965), Weatherley (1963, 1972) and Nikolsky (1969) discussed the concept in relation to freshwater fish, whilst Nilsson (1967b) discussed the related topic, interactive segregation (Brian, 1956a), as it applies to fish species. In the present study, the definition of Clements and Shelford (1939:159) as modified by Miller (1967; see also Weatherley, 1972) is used. This definition states that "biological competition is the active demand of two or more individuals of the same species population (intraspecies competition) or members of two or more species at the same trophic level (interspecies competition) for a common resource or requirement that is actually or potentially limiting." Thus, interspecific competition is here distinguished from "competition for a niche" between species. The latter phenomenon may include not only competition for food, space etc., but also such mechanisms as predation by the competitors on each other and "competition for survival under the influence of predation, parasitism or any other factors of environment which differentially affect the competitors" (Larkin, 1956).

Interspecific relationships are considered under the headings: space, spawning sites and food.

1. Spatial Relationships

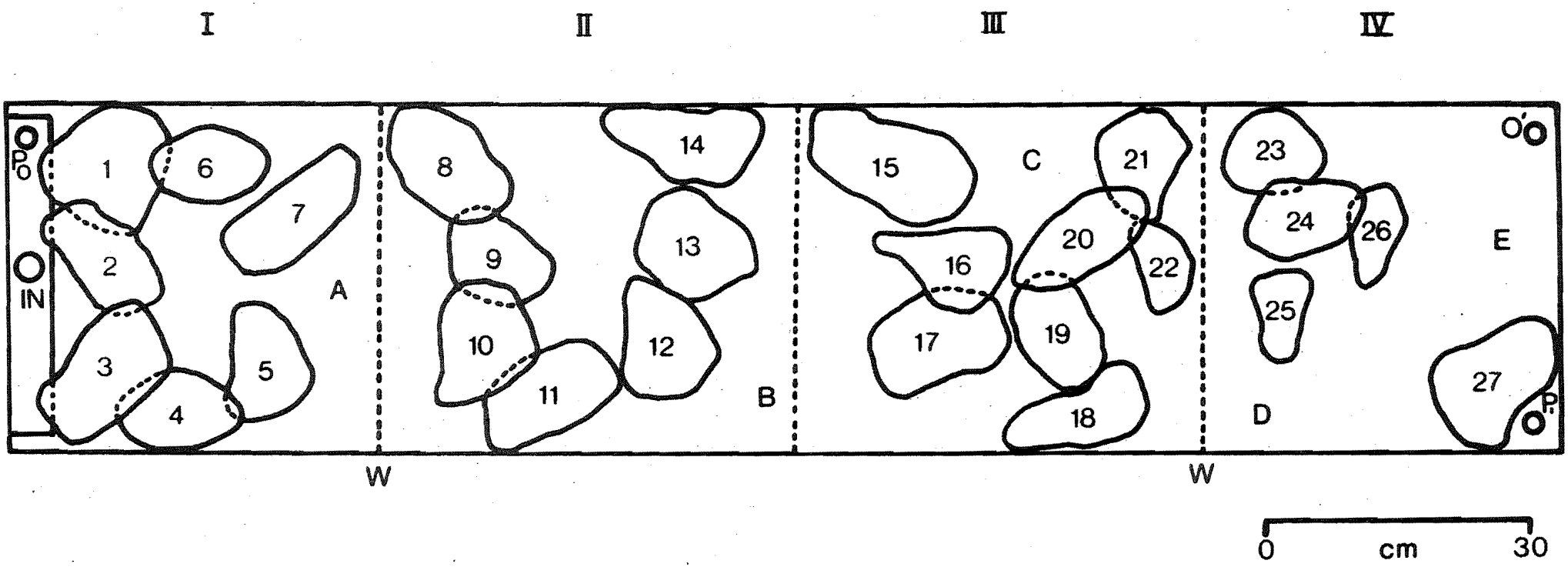
(1) Distribution of fish within the River Glentui

As pointed out in Chapter IV, recently-hatched G. vulgaris

occur in the quiet parts of the River. On reaching a length of about 40 mm they move into riffle areas, the normal adult habitat. Galaxias vulgaris longer than 50 mm were only rarely found in areas other than riffles. Within the riffle areas, fish were normally found in the more turbulent areas, with the largest fish occupying the most turbulent parts, normally at the heads of the riffles. Chapman and Bjornn (1969) reported a similar situation in juvenile chinook salmon, Oncorhynchus tshawytscha, and steelhead trout, Salmo gairdneri. At certain times of the year, these fish were associated with velocities and depths proportional to their body size, moving to faster and deeper water with increase in size. The role of territoriality in the distribution of G. vulgaris within the riffle areas is indicated by observations made in a stream tank (see section 1.(2)(b) of this Chapter).

Philyponodon breviceps was generally distributed throughout the River, both in riffle areas and quiet stretches (see Table 19). As with recently-hatched G. vulgaris, recently-hatched P. breviceps were found in the more quiet parts. However, the spawning season of P. breviceps occurred later than that of G. vulgaris (see section 2. of this Chapter), so there was no overlap of large numbers of recently-hatched G. vulgaris and P. breviceps in the same areas. Woods (1967, unpublished) indicated that only juveniles and younger fish were regularly found in areas which offered little shelter: adult P. breviceps were found in areas provided with cover, in the form of stones, but the microhabitat of males and females differed. Males were usually found under stones, whereas females occurred between stones or on shingle which provided little cover. In the River Glentui, adult P. breviceps were found to occupy the quieter parts of the riffles, whereas G. vulgaris, as mentioned above, was found in the more turbulent parts. However, in the sections of the River from which samples of G. vulgaris were regularly removed, P. breviceps occurred in increasing numbers in the more turbulent areas, i.e. in the areas which were normally occupied by G. vulgaris. This observation suggested that interactive segregation was occurring between the adults of G. vulgaris and P. breviceps in the riffle areas of the River, i.e. under normal conditions (without the interference of the investigator), G. vulgaris and P. breviceps were segregating into

FIGURE 49. The stream tank. See section 1.(2)(a) for description.


I
II
III
IV
O
IN
O'
P'
1
2
3
4
5
6
7
A
8
9
10
11
12
13
14
B
15
16
17
18
19
20
21
22
C
23
24
25
26
27
D
E
W
W
0
cm
30

different parts of the riffle as a result of competition and/or predation (see Nilsson, 1967b). Miyadi et al (1952, in Kawanabe, 1959) reported a similar situation in a Japanese river in which pale chub, Zacco platypus, inhabited the central parts of riffles when Ayu, Plecoglossus altivelis, was absent. However, when the Ayu ascended the river, the chub was restricted to the river margins or the boundaries between riffles and pools: when the Ayu descended the river, the chub returned to its former habitats. Nilsson (loc. cit.:294) presents a number of examples in which the ecology and behaviour of fish species differ when coexisting and when living separately.

Large trout (>20 cm long) were uncommon in the River Glentui: when they did occur they were found in deep channels and pools. Trout smaller than 20 cm were normally taken in riffle areas, usually in the more turbulent areas, where they sheltered between large boulders, a microhabitat similar to that of G. vulgaris. Large eels were normally found beneath overhanging banks and in deep pools with plenty of cover, whilst the smaller eels (up to 30 cm long) often occurred beneath boulders: Burnet (1955, unpublished) reported similar findings for eels in other Canterbury rivers.

(2) Laboratory observations

Investigations into the spatial interactions of G. vulgaris and P. breviceps, the two most numerous fish species in the River Glentui, were made in a stream tank: the spatial interactions of G. vulgaris and S. trutta were also examined, but in less detail.

(a) The stream tank

Stream tanks of technical necessity are extremely simplified versions of the real situation. They permit investigation of a few components at a time, without the complex of interactions which characterize the natural system. However, as pointed out by Warren and Davis (1971) in a recent review of laboratory stream research, careful consideration is needed when applying the results of stream tank investigations to the real situation.

The stream tank used in the present study (see Fig. 49) was made of wood waterproofed with "Epiglass" and had the following internal dimensions: 189 cm long, 42.5 cm wide and 30 cm deep. Two observation windows (W) (83.5 x 19 cm) enabled the investigator to view all parts

of the tank. The water inlet (IN), which was positioned along one of the end walls of the tank, consisted of a cylinder of P.V.C., 36 cm long, sealed at both ends, with a slit (S), 5 mm deep, along the length of the outward-facing side. Water reached the inlet through a P.V.C. pipe connected to the upper surface of the inlet and entered the tank, via the slit, along the whole length of the cylinder. The outlet (O^{1}), situated at one downstream corner of the tank, consisted of a hole in the base of the tank surrounded by a cylinder of wire gauze which stood 18 cm high. At the other downstream corner, a similar cylinder surrounded the inlet pipe (P^{1}) of a pump which continually recycled about one third of the volume of water in the tank at any one moment. The outlet of the pump (Po) was situated above the inlet cylinder at the upstream end of the tank. Maximum current velocities in different parts of the tank were 25.3 cm/sec at position A (see Fig. 49), 16.8 cm/sec at B, 18.6 cm/sec at C and 4.6 cm/sec at D and E. The tank was nominally divided into four sections (I, II, III and IV) and was provided with moveable screens (whose positions are indicated by the dotted lines in Fig. 49) which could be lowered into position, if necessary, thereby isolating each of the four sections. The substrate consisted of gravel (particle size <3 mm, depth <6 mm) and boulders (numbered 1 - 27 in Fig. 49). Because of the action of the inflowing water, no gravel was present immediately beneath the inlet or beneath boulders 1, 2 and 3. The tank was inclined at an angle of 3^{o} to the horizontal, so that the water depth varied between 5 cm at the upstream end and 9 cm at the downstream end.

(b) Experimental investigation of the spatial interactions of *G. vulgaris* and *P. breviceps*

i. Preliminary observations

Observations on *G. vulgaris* in the stream tank indicated that although they did not have a distinct patrolled territory they appeared to have a "diffuse station territory" of the type described by Kalleberg (1958). As Kalleberg pointed out, the number of such territories on the stream bed may depend on the topography of the bottom, with more territories potentially available in areas where there are plenty of obstacles

to prevent visual contact between fish. However, as indicated by Chapman (1966), since the supply of drift passing a given point is proportional to water velocity, it is conceivable that drift-feeders require less space to guarantee adequate food when velocities are high. Since rubble is usually associated with rapid flows, the two factors probably exert complementary effects on the size and, therefore, the number of territories. In G. vulgaris, "stations" were maintained only at night: during the day, fish sheltered beneath boulders and up to three fish were often seen under the same boulder.

Philypnodon breviceps demonstrated a more rigid intraspecific territorial system than G. vulgaris. Dominance depended on size and since males were larger than females they tended to have the more settled territories. As a result of this size hierarchy males were generally found beneath boulders and females were generally found in open water between boulders, supporting the observations made by Woods (1967, unpublished) for the natural situation (see section 1.(1) above).

As a prerequisite to investigating the distributions of two different species in single-species and mixed-species situations, it was necessary to demonstrate that groups of individuals of each species would maintain a similar distribution in the stream tank on two separate occasions. For this purpose, a group of four individuals was placed in the stream tank for 10 days and, after a three-day acclimatization period, its distribution was recorded at intervals, at least one hour apart; it was then removed from the stream tank. After one week, it was replaced into the stream tank and, after a three-day acclimatization period, its distribution was again recorded over a period of one week. This trial was performed twice with G. vulgaris and twice with P. breviceps. The G-test (Sokal and Rohlf, 1969) was used to compare the two distributions in each trial (see Table 44). It may be seen that for both trials in each species, the two distributions were not significantly different ($p > 0.05$). The similarity of distributions after a period of one week's absence from the stream tank probably reflects similar reactions to the same situation, rather than memory. In either case, the trials demonstrate the ability of both species to occupy similar positions

in the stream tank on two occasions separated by a period of one week.

TABLE 44 Values of G for comparisons of the distributions of groups of four individuals kept in the stream tank on two separate occasions t_1 and t_2 (n = number of fish observations).

	Trial	t_1, n	t_2, n	G(d.f. = 3)	Signif.
G. vulgaris	1	80	80	6.493	NS
	2	100	100	5.020	NS
P. breviceps	3	80	80	6.442	NS
	4	120	100	7.317	NS

NS = not significant

ii. Experimental procedure

Eight experiments were performed with the object of examining the distribution of G. vulgaris and P. breviceps in single-species and mixed-species situations. The investigations were carried out under normal night-day conditions and the water temperature in the stream tank throughout the experiments ranged from 11° to 13.5° C. All fish carried individually-recognizable Alcian Blue marks, administered with a jet inoculator (see Chapter I). In each experiment, one group of individuals of species A was initially placed into the stream tank and allowed three days to acclimatize to the experimental conditions. After the acclimatization period, the distribution of each fish was recorded on 20 - 30 separate occasions, observations being at least one hour apart. After this first set of observations, species A was removed from the stream tank and replaced by a group of individuals of species B. After a three-day acclimatization period, the distribution of species B was recorded in a similar way to that of species A. Immediately after the last observation in this second set of observations, species A was reintroduced into the stream tank, so that now the two species were together. After a three-day acclimatization period, the distribution of each individual of each species was recorded in a similar manner to that used in the two previous sets of observations.

Thus, the distribution of individual fish of each species was examined in single-species and mixed-species situations.

All fish placed in the stream tank were released from a hand-net, facing downstream, at the junction of sections II and III. To overcome any bias introduced by different activity patterns of the two species under investigation, equal numbers of day and night observations were made. The day observations were made without any disturbance of the stream tank. However, preliminary investigations indicated that the switching on of artificial lights in order to make night observations often disturbed the fish and caused them to change their positions. Therefore, before making observations at night, screens (see section 1.(2)(a) of this Chapter and Fig. 49) were lowered into the stream tank before switching on the artificial lights, thereby confining the movements of any disturbed fish to the section in which they happened to be at the time of the lowering of the screens. Experimental fish not in the stream tank were held, in their groups, in running-water aquaria, a separate aquarium being used for each species. Fish were fed every other day in the holding aquaria, but were not fed in the stream tank. Thus, group B went without food for a longer period than group A during the course of each experiment. Any effects of this differential starvation, together with any possible effects of prior residence on the outcome of interspecific encounters, were partly taken into account by alternating the species which was first placed into the stream tank. That prior residence may be important in deciding the outcome of dominance interactions, at least between members of the same species, is indicated by the work of Braddock (1949), Miller (1958) and Timmermans (1961).

Since it took about one week to complete each set of observations in each experiment, experiments normally lasted for 30 days. Four individuals of each species, two fish of each sex, were used in each experiment, except in experiment 1, in which six individuals of each species were used. However, four G. vulgaris died during the course of experiments and were excluded from subsequent analyses. All of the fish died of Saprolegnia sp. infections whilst in the holding tanks. Different fish were used in each experiment. The mean length of the

G. vulgaris used in the experiments was 84.9 mm ($s.\bar{y}$ = 2.06) and the mean length of the P. breviceps used was 68.0 mm ($s.\bar{y}$ = 1.48).

The experimental procedure may be summarized as:

1. Species A in stream tank, species B in holding tank
   i. three-day acclimatization period
   ii. 20 - 30 observations on the distribution of each fish.
2. Species B in stream tank, species A in holding tank
   i. three-day acclimatization period
   ii. 20 - 30 observations on the distribution of each fish.
3. Species A and species B in stream tank
   i. three-day acclimatization period
   ii. 20 - 30 observations on the distribution of each fish.
   iii. Results

Although only 34 P. breviceps and 30 G. vulgaris were used in the eight experiments, the analysis included 3,562 individual fish-observations.

TABLE 45 The percent distribution of all G. vulgaris (30 fish) and all P. breviceps (34 fish) in single-species situations. (Data from eight experiments combined). (n = number of fish-observations; I, II, III, IV represent stream tank sections, where I is the upstream section and IV is the downstream section (see Fig. 49)).

	n	I	II	III	IV
G. vulgaris	848	73	16	8	3
P. breviceps	912	52	21	11	16

The distributions of all G. vulgaris and all P. breviceps in single-species situations is shown in Table 45. The G-test indicates that the two distributions are non-random (for G. vulgaris, G = 414.458, d.f. = 3, $p<0.005$; for P. breviceps, G = 89.230, d.f. = 3, $p<0.005$) and are significantly different from each other (G = 36.716, d.f. = 3, $p<0.005$), although both species exhibited a preference for the upstream end of the tank.

TABLE 46. Values of G for comparisons of the distributions of individual G. vulgaris (Gv) and P. breviceps (Pb) in single-species and mixed-species situations. (sp.A = the species which was placed into the stream tank first; nM = the number of observations made on each individual in mixed-species situations; nS = the number of observations made on each individual in single-species situations; d.f. = degrees of freedom). See text of section 1.(2)(b) for an explanation of the experimental procedure.

				G. vulgaris				P. breviceps				
				Males		Females			Males		Females	
Expt.	sp.A	nM	nS	G(d.f.=3)	signif.	G(d.f.=3)	signif.	nS	G(d.f.=3)	signif.	G(d.f.=3)	signif.
1	Gv	24	26	2.465[1]	NS	5.636[1]	NS	20	8.526[1]	*	20.463[1]	***
				15.361[2]	***	+	-		8.480[2]	*	4.432[2]	NS
				+	-	+	-		16.105[3]	***	16.003[3]	***
2	Pb	30	30	88.635	***	-0.969	NS	30	47.403	***	26.282	***
				26.767	***	12.681	**		54.593	***	24.150	***
3	Gv	30	30	7.214	NS	24.632	***	28	9.239	*	12.006	**
				11.962	**	3.791	NS		36.243	***	9.758	*
4	Pb	28	30	6.483	NS	4.237	NS	30	25.824	***	3.218	NS
				8.592	*	2.622	NS		114.962	***	11.949	**
5	Gv	26	24	43.261	***	17.010	***	30	63.819	***	12.927	***
				3.722	NS	13.460	***		72.916	***	36.465	***
6	Pb	30	30	12.492	*	+	-	30	13.492	***	27.233	***
				4.176	NS	2.629	NS		8.898	*	15.101	***
7	Gv	30	30	2.986	NS	63.576	***	30	11.260	*	9.744	*
				13.020	***	12.212	**		52.310	***	14.279	***
8	Pb	28	26	2.107	NS	3.074	NS	20	45.667	***	7.323	NS
				18.392	***	1.438	NS		19.213	***	26.734	***

+ = fish died during experiment, excluded from analysis
NS = distributions not significantly different
*, **, *** = distributions significantly different at the 0.05, 0.01 and 0.005 probability levels respectively
1, 2, 3: these figures refer to the correspondingly-numbered histograms in Fig. 50

FIGURE 50. Stream tank experiment 1 : distributions of individual G. vulgaris and P. breviceps in single-species (s) and mixed-species (m) situations. (I, II, III, IV represent stream tank sections, where I is upstream and IV is downstream; n = number of fish-observations on which each histogram is based; M = male; F = female). See text of section 1.(2) for further explanation.

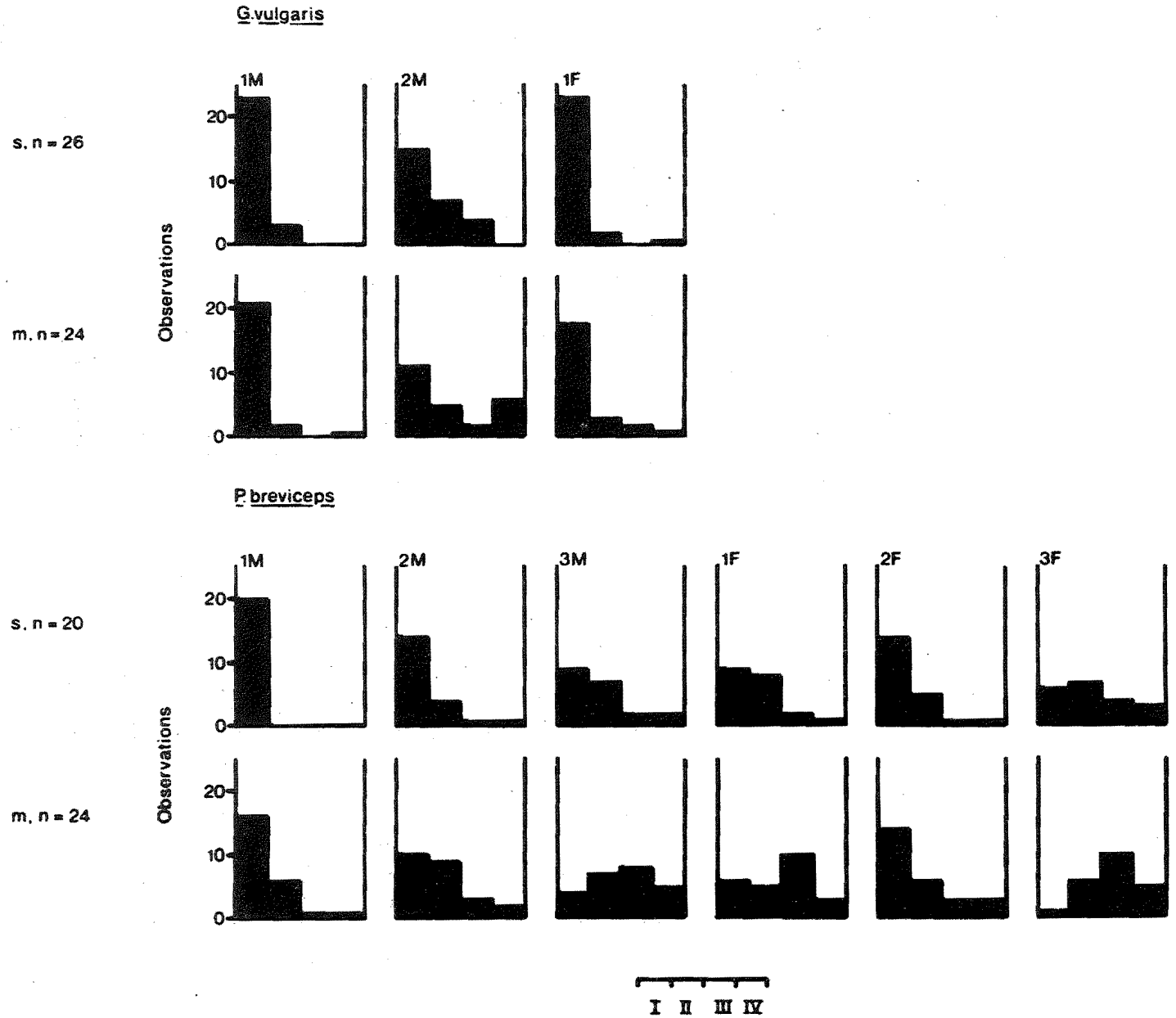
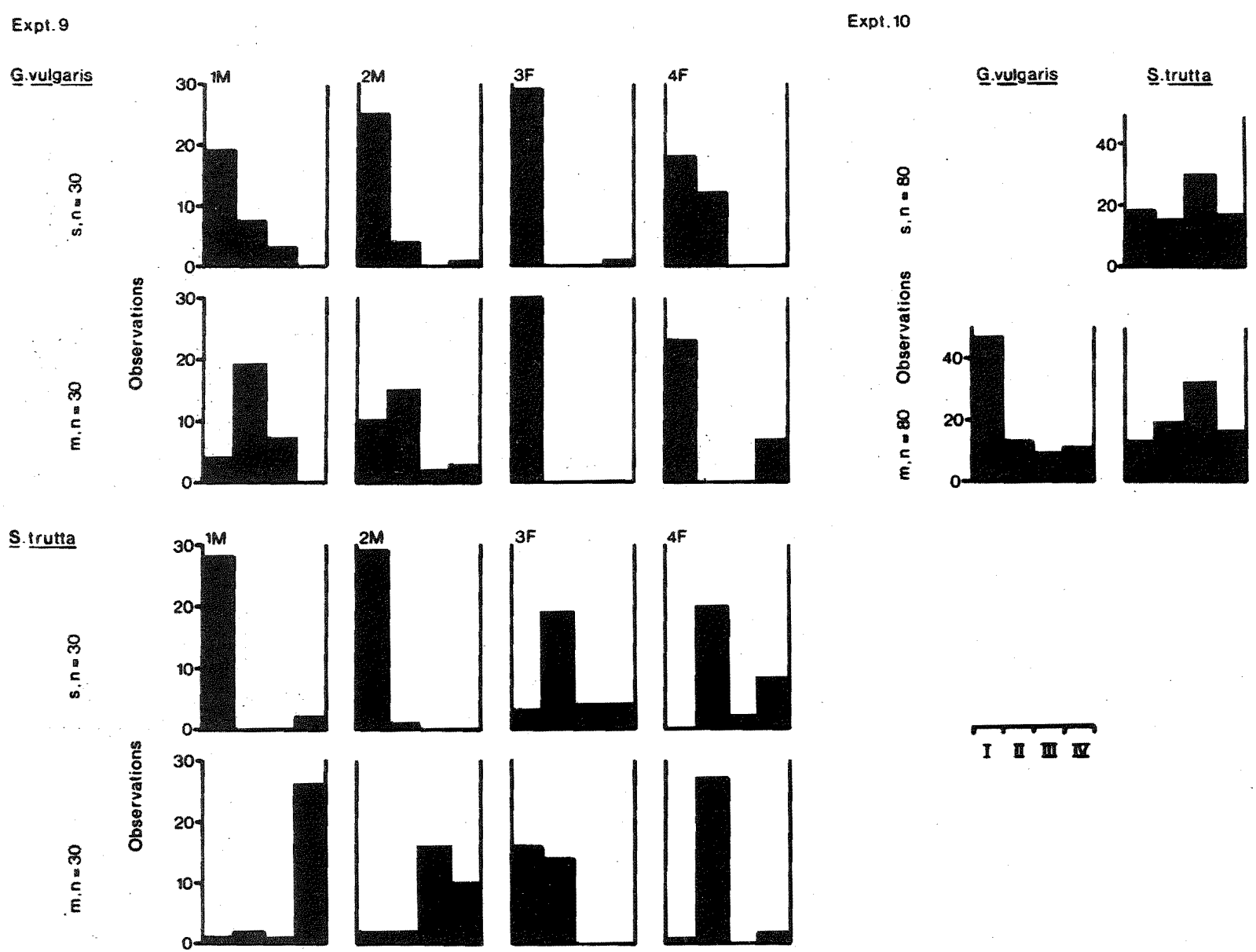

G.vulgaris
1M
2M
1F
s, n = 26
m, n = 24
Observations
20
10
0
P breviceps
1M
2M
3M
1F
2F
3F
s, n = 20
m, n = 24
Observations
20
10
0
I II III IV

FIGURE 51. Stream tank experiments 9 and 10: distributions of G. vulgaris and S. trutta in single-species (s) and mixed-species (m) situations. (I, II, III, IV represent stream tank sections, where I is upstream and IV is downstream; n = number of fish-observations on which each histogram is based; M = male; F = female). See text of section 1.(2) for further explanation.


Expt. 9
G. vulgaris
S. trutta
1M
2M
3F
4F
s, n = 30
m, n = 30
Observations
0
10
20
30
Expt. 10
G. vulgaris
S. trutta
s, n = 80
m, n = 80
Observations
0
20
40
I
II
III
IV

Values of G for comparisons of the distributions of each individual fish in single-species and mixed-species situations are presented in Table 46. It may be seen that significant differences occurred in the distributions of individuals of both species in mixed-species situations compared with single-species situations. However, the differences were more marked in P. breviceps than in G. vulgaris. In the eight experiments, only three P. breviceps (out of 34) had distributions in single-species and mixed-species situations which were not significantly different, whereas 15 (out of 30) G. vulgaris had distributions in single-species and mixed-species situations which were not significantly different. The distributions of each individual in experiment 1 are presented in Fig. 50 as an example of the changes in distribution which occurred between single-species and mixed-species situations.

(c) Experimental investigation of the spatial interactions of G. vulgaris and S. trutta

Two experiments of a preliminary nature were carried out in order to investigate the spatial interactions of G. vulgaris and S. trutta in the stream tank. In the first experiment (stream tank experiment 9), involving four G. vulgaris of mean length 94.3 mm ($s.\bar{y}$ = 7.58) and four S. trutta of mean length 95.5 mm ($s.\bar{y}$ = 1.09), the procedure was identical with that used in the experiments to investigate the spatial interactions of G. vulgaris and P. breviceps, with G. vulgaris being placed first into the stream tank. In the second experiment (stream tank experiment 10), involving four G. vulgaris of mean length 91.5 mm ($s.\bar{y}$ = 2.93) and four S. trutta of mean length 48.5 mm ($s.\bar{y}$ = 1.15), fish were not individually marked; the distribution of the S. trutta was recorded in a single-species situation, the G. vulgaris group was then introduced into the stream tank and the distribution of the S. trutta was again recorded. The acclimatization periods and the method of making observations were the same as those outlined in section 1.(2) (b) ii. of this Chapter.

The distributions of the fish in each experiment are shown in Fig. 51; the values of G for comparisons of the distributions in single-species and mixed-species situations are presented in Table 47.

TABLE 47 Values of G for comparisons of the distributions of *G. vulgaris* and *S. trutta* in single-species and mixed-species situations. (nM = the number of observations made on each individual in mixed-species situations; nS = the number of observations made on each individual in single-species situations; M = male; F = female. *S. trutta* were sexed after dissection at the end of each experiment).

Expt. 9: nM = 30; nS = 30

	S. trutta			*G. vulgaris*	
No.	G(d.f. = 3)	Signif.	No.	G(d.f. = 3)	Signif.
1M	129.486	***	1M	2.034	NS
2M	126.850	***	2M	50.193	***
3F	45.017	***	3F	32.267	***
4F	10.660	***	4F	30.691	***

Expt. 10: nM = 20; nS = 20

S. trutta (4F): G = 2.813 (d.f. = 3), NS

G. vulgaris (2M, 2F): only present in mixed-species situation

NS = distributions not significantly different

*** = distributions significantly different at the 0.005 probability level

It may be seen that with the larger trout (experiment 9), the distributions in single-species situations were significantly different from the distributions in mixed-species situations. Similarly, in the same experiment, all except one of the paired distributions of *G. vulgaris* were significantly different. The distribution of the smaller trout (experiment 10) was not significantly different in single-species and mixed-species situations.

(d) Factors affecting the interpretation of the results of the stream tank experiments

The major criticism of the stream tank investigations is the lack of simultaneous control experiments. Since only one stream tank was available the experimental results were, of necessity, compared with control results (for *G. vulgaris* and *P. breviceps*) obtained at an

earlier date (i.e. with the results obtained in the preliminary single-species trials 1 - 4).

In single-species situations, the preference shown by most groups of fish for the upstream end of the stream tank may be explained, at least in the case of G. vulgaris, by an attempt to reach their home range, rather than a choice of a turbulent area as opposed to a quiet area. Artificial displacement of G. vulgaris to an area in which they receive no stimuli from their home range normally results in an upstream movement (see Chapter V). However, the three-day acclimatization period was considered sufficient to overcome any disorientation of the fish: after this period, fish did not appear to be trying to move further "upstream".

The performance of the different species may have been affected by differential reactions to the experimental situation. Also, the densities used in the experiments, normally eight fish per 0.8 m^2, were higher than the densities found in the River Glentui. The number of encounters would therefore probably be higher than in the natural situation.

(3) Discussion

The results obtained in the laboratory investigations indicate that interactive segregation between G. vulgaris and P. breviceps occurred in the stream tank. In single-species situations, both species showed a preference for the upstream end of the stream tank. In mixed-species situations, the distributions changed, although it was shown that groups of fish of either species were capable of maintaining similar distributions in single-species situations on two separate occasions one week apart. In mixed-species situations, the distributions of individual P. breviceps were more affected than those of G. vulgaris. It is of interest that the distributions of all male P. breviceps were significantly different: these fish were normally found beneath boulders in the upstream section of the tank (beneath boulders 1, 2 and 3), positions also favoured by G. vulgaris. Female P. breviceps were more evenly distributed throughout the tank and this may explain the fact that three of the female distributions were not significantly different in single-species and mixed-species situations.

Interspecific encounters were observed on two occasions in the stream tank. On the first occasion, a G. vulgaris chased a P. breviceps from beneath a boulder, whilst on the second occasion a G. vulgaris chased a P. breviceps, which was swimming above the galaxiid, for about 30 cm. Also, in a small aquarium (40 x 30 x 20 cm) in the spawning season, a female G. vulgaris, 77 mm long, was seen to bite a male P. breviceps, 70 mm long. Eldon (1969) reported that in small aquaria G. vulgaris was aggressive towards mid-water species such as smelt, Retropinna retropinna, but "shy of bottom-dwellers" such as Gobiomorphus huttoni, a species with similar habits to those of P. breviceps. In the present study, observations of intraspecific encounters in G. vulgaris indicated that fish were normally only aggressive in open water and were, therefore, likely to be more aggressive when feeding than when not feeding. The relationship between aggression and feeding is discussed further in section 3. of this Chapter.

Interspecific aggression is common amongst salmonids, which have a number of elements of their threat displays in common (Newman, 1956; Kalleberg, 1958; Hartman, 1965). Hartman (loc. cit.) demonstrated that when underyearling coho salmon, O. kisutch, and steelhead trout, S. gairdneri, were in experimental riffle and pool environments, trout were aggressive and defended areas in riffles but not in pools, whereas salmon were aggressive in pools but less inclined to defend space in the riffles. It was suggested that these differences in behaviour probably accounted for the distribution of the trout and salmon in natural riffles and pools. Hankinson (1932) reported an instance of interspecific aggression, in which a hornyhead, Nocomis biguttatus, attacked a hammerhead sucker, Hypentelium nigricans, causing it to retreat from the former's nest site, even though the hornyhead was only one quarter of the size of the sucker. Smyly (1957) noticed that in aquaria, Cottus gobio would not share the same stone as the loach, Nemacheilus barbatula, although both species normally live beneath stones. He quoted a personal communication which suggested that in a river in which both species were common, they were segregated, such that in areas where one was abundant the other was rare. Winn (1958) noted that many species of darter (Percidae) interact with one another, exhibiting interspecific defence of territories. Interspecific aggression

has also been reported between S. trutta and the bullhead C. gobio, and Salmo salar (Lindroth, 1955); between the sculpin Cottus beldingi and brook trout, S. fontinalis (Needham and Jones, 1959); and between the Ayu, P. altivelis, and the goby, Rhinogobius similis (Kawanabe, 1959). More recently, Johnson and Peeke (1972) working on intra- and interspecific aggression of five species of labyrinth fish (Belontiidae) and a catfish, Corydoras reticulus, in experimental situations, found that intraspecific aggression occurred much more frequently than interspecific aggression and that reducing the amount of available space, thereby increasing the density of fish, resulted in an increase in both intra- and interspecific aggression.

As pointed out by Nilsson (1967b), interspecific avoidance may be released by stimuli other than aggression, for example, by strange sizes, colours, movements, sounds or odours. He cites the work of Breder (1929) who found that alien species passing through shoals of Jenkinsia stolifera caused "empty spaces" around themselves, i.e. individuals of J. stolifera avoided approaching the strangers. In this respect, Eldon's (1969) observation that G. vulgaris are "shy of bottom-dwellers" may be significant. Also, Ivlev (1961) found that, when keeping mixed-species groups of fish in aquaria divided into inter-connecting sections by transparent and opaque screens, only one species of fish occurred in each section, despite the fact that the experimental species were "non-aggressive" types.

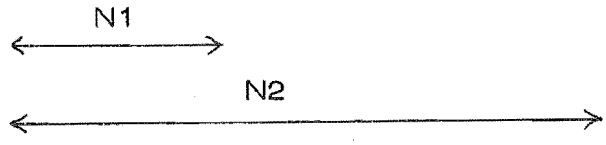
Whether the type of interactions between G. vulgaris and P. breviceps observed in the stream tank actually occur in the natural situation is unknown. Nevertheless, the observation that when G. vulgaris is removed from the River, P. breviceps tends to increase in numbers in the areas previously occupied by G. vulgaris, suggests that some interactive mechanism is at work. No information was obtained of the effect on the distribution of G. vulgaris, if P. breviceps was removed from the riffle areas. However, the habitat requirements of G. vulgaris appear to be much more stringent than those of P. breviceps which occurs in all types of water, both lotic and lentic (Cranfield, 1962, unpublished; Woods, 1967, unpublished; Lane and Skrzynski, 1972). Stokell (1955) noted that P. breviceps showed "remarkable adaptability to different types of habitat." He transferred specimens from a rapid

alpine stream to a small land-locked lake which previously contained no native fish: P. breviceps immediately adapted to the new conditions and "multiplied so rapidly that the lake was fully stocked in three years." On the other hand, G. vulgaris is found only in the riffle areas of streams and rivers and does not occur in lakes (Stokell, 1949, 1955; Hopkins and McDowall, 1970; McDowall, 1970; Lane and Skrzynski, 1972). Stokell (1949, 1955) transferred "some hundreds of specimens" of G. vulgaris into a small lake fed by seepage from a number of small streams which did not normally flow directly into the lake. He found that the fish existed in the lake for about one year, but "escaped" into the largest tributary during a period of connected water and have "remained there ever since." In the River Glentui P. breviceps was capable of occupying all sections of the riffles, whereas G. vulgaris occupied only the more turbulent areas and was only rarely found in the quiet parts of the riffles. Furthermore, P. breviceps was often found in parts of the River other than riffles, provided cover was present in the form of boulders. Apart from recently-hatched fish and juveniles, G. vulgaris was found only on rare occasions in the quiet parts of the River.

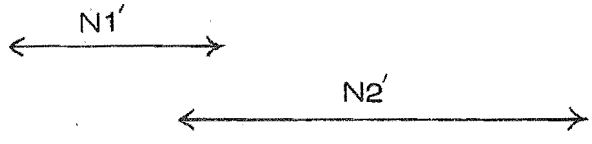
Exploitation, i.e. "the ability of a species to find, occupy and retain vacant vital resources" (Brian, 1956b), does not fully explain the situation in the River Glentui. Interference (i.e. "the ability of a species to damage another (assuming for simplicity that there are only two) either directly by attacking its individuals or indirectly by harming its resources or blocking its access to them") (Brian, loc. cit.) between the two species is most probably important in determining their spatial distribution. Galaxias vulgaris appears to be the more dominant species in the stream tank in situations in which the two species compete for the same microhabitat. This situation probably also occurs in the River Glentui.

Philypnodon breviceps may therefore be regarded as a relatively unspecialized fish as far as distribution is concerned, whereas the requirements of G. vulgaris are rather more stringent. Although P. breviceps may occupy all parts of a riffle in the absence of G. vulgaris, it is restricted to the quieter parts when G. vulgaris is present. The niche relationships of G. vulgaris and P. breviceps, as far as spatial

requirements are concerned, appear to be an example of Miller's (1967:21) type C relationship of fundamental niches (i.e. the niches that might be expressed in the absence of competitive interaction), which may be represented as:



where N1 is the fundamental niche of G. vulgaris and N2 is the fundamental niche of P. breviceps, the niches being represented for simplicity by single variables (in this instance, spatial requirements). In the River Glentui, the realized niche (i.e. the niche that is occupied when competition restricts the expression of the total species potential) of G. vulgaris is apparently very similar to its fundamental niche (although there is no direct evidence for this, other than from the stream tank experiments), whereas the realized niche of P. breviceps is smaller than its fundamental niche. The realized niches of G. vulgaris and P. breviceps in the River Glentui, as far as spatial requirements are concerned, may be represented as:



where N1′ and N2′ are the realized niches of G. vulgaris and P. breviceps respectively. Miller (loc. cit.) cites a number of examples of this type of situation.

Although interference appears to occur between G. vulgaris and P. breviceps, exploitation alone may explain the spatial segregation of a number of other fish species. For example, although recently-hatched leopard dace, Rhinichthys falcatus, and longnose dace, Rhinichthys cataractae, occur together in regions of quiet water, older R. cataractae soon begin to occupy situations with high water velocity, whereas older R. falcatus remain predominantly in quiet areas (Gee and Northcote, 1963). Laboratory stream tank experiments indicated a strong current preference in R. cataractae, whereas R. falcatus of comparable size exhibited no preference for water current. The swimbladder volume of R. cataractae was found to be much lower than that of R. falcatus and Gee and Northcote (loc. cit.) suggested that this was possibly an adaptation of R. cataractae to occupation of a riffle habitat.

Lister and Genoe (1970) found that the habitat preferences of chinook, O. tshawytscha, and coho salmon, O. kisutch, during the first three months of stream life were similar. With increased size, the fish moved into situations of progressively higher velocity. However, differences in time of emergence and size evidently resulted in the spatial segregation of the two species. Chinook fry emerged about one month earlier than coho fry, were larger at emergence and grew at a faster rate. Apparently, because of their larger size at a given time, chinook preferred locations of higher velocity than coho. Similarly, Griffiths (1972) found that yearling and older cutthroat trout, S. clarki, and brook trout, S. fontinalis, occupied territories whose focal points were at different mean water velocities, although there was considerable interspecific overlap in other habitat characteristics.

The spatial interrelationships between S. trutta and adult G. vulgaris appear to depend on the size of the trout. In the stream tank, small trout (mean length = 48.5 mm) appeared to prefer areas different from those preferred by the larger trout (mean length = 95.5 mm), and were found mainly in Section III. The larger trout appeared to favour similar situations to those preferred by G. vulgaris. Although only one experiment was performed (experiment 9), it was found, with one exception, that the distributions of the individuals of each species were significantly different in single-species and mixed-species situations, indicating that some type of interaction was occurring. However, the distributions of the group of small trout in single-species and mixed-species situations (experiment 10) were not significantly different. This may be explained by the fact that the preferred distribution of the small trout in the stream tank (see Fig. 51) was in areas not normally occupied by G. vulgaris, although on one occasion, a G. vulgaris male, 90 mm long, was seen to chase one of the trout for a distance of about 30 cm. Although only of a preliminary nature, the experiments with G. vulgaris and S. trutta indicate that some size-groups of trout may interact competitively with G. vulgaris. The opportunity for competitive interactions is increased by the similarity in activity patterns of G. vulgaris (see Chapter VI) and S. trutta. Chaston (1968b) demonstrated that S. trutta is active mainly at night. Also, in the present study, measurement of the spontaneous locomotory activity of a single S. trutta 49 mm

long (using the apparatus described in section 3.(1) of Chapter VI), indicated that activity was generally higher at night than during the day (diel activity ratio (based on mean hourly values for a three-day period) = 1.3), with a peak after sunset.

No experiments were conducted on the relationships between S. trutta and P. breviceps, although it is likely that the spatial requirements of the two species may overlap at some stage of their life cycles.

2. Competition for Spawning Sites

As pointed out by Lagler (1944) competition between species for spawning sites may lead to reduction in reproductive success of the least aggressive species, or, in closely related forms, hybrids may be produced (Bailey and Lagler, 1938; Reighard, 1943). Since spawning occurs infrequently in most fish species, competition for spawning sites would be expected to occur much less frequently than competition for other resources such as food and resting places which are continually in demand. However, as indicated by Larkin (1956), the effect on the losing species of competition for spawning sites will be much more detrimental to the population than "occasional and temporary competition for food."

In the River Glentui, competition for spawning sites did not occur. Eels do not reproduce in fresh water: Castle (1963) suggested that the New Zealand freshwater eels spawn somewhere in the tropical Pacific, northwest of the New Hebrides. The spawning habits of S. trutta in New Zealand are essentially the same as those of brown trout in the Northern Hemisphere (Percival, 1932; Hobbs, 1937, 1940, 1948; Allen, 1951). No redds were found within the sampling area in the River Glentui during the present study (field observations were made mainly between June 1970 and April 1972), but the spawning requirements of S. trutta suggest that competition for spawning sites between it and the native fish does not occur.

The spawning habits of P. breviceps have been mentioned by Stokell (1955), Cranfield (1962, unpublished), Burnet et al (1969) and Staples (1971, unpublished) and appear to be similar in all bullies of the genera Gobiomorphus and Philypnodon (Hopkins and McDowall, 1970).

The oval stalked eggs are laid in a single layer on flat undersurfaces of rocks and are usually guarded by a single male. Twelve nests of P. breviceps were found in the River Glentui; all were found at the sides of the main channel in the quiet parts of the River, in areas such as U3, U1, D1 and D3 of the home range investigation (see Fig. 23). Nests of G. vulgaris were normally found on gravel beneath boulders in riffle areas (see Chapter IV). Furthermore, spawning of P. breviceps occurred in summer (November - December), whereas spawning of G. vulgaris took place in late winter and early spring. Competition for suitable spawning sites is therefore not a factor to be considered in the relationships of the two species in the River Glentui. However, Benzie (1961, unpublished) reported an interesting observation in the Cass River, where, in October, a mass of G. vulgaris eggs was found beneath the same stone as a batch of P. breviceps eggs which was being ventilated by a male; three G. vulgaris, all males, were found nearby. Spawning of G. vulgaris in the Cass River, as mentioned in Chapter IV, occurs later than in the River Glentui, so that the spawning seasons of the two species overlap in this locality. In such circumstances, although G. vulgaris normally deposits the egg mass on gravel beneath a rock and P. breviceps eggs are found on the underside of a rock, it is conceivable that the selection of the same rock by individuals of both species could lead to interspecific encounters, with only one species succeeding in spawning at the site. This does not appear to be the case in the situation outlined above.

3. Feeding Relationships

Feeding relationships of the fish in the River Glentui will be discussed after a consideration of the role of interspecific competition for food in freshwater fish communities in general.

(1) Feeding relationships of fish at the same trophic level

A large number of workers (e.g. Van Oosten and Deason, 1938; Calhoun, 1944; Butcher, 1945; Leonard and Leonard, 1949; Frost, 1950; Hunt and Carbine, 1950; Hynes, 1950; Lachner, 1950; Larsen, 1967; Munro, 1967; Sinha and Jones, 1967; Cragg-Hine and Jones, 1969; Lackey, 1969; Mann and Orr, 1969; Fagade, 1971) have found that two or more fish species in the same community have similar diets, although

the relative proportions of the various items in the diets often vary between species. Such similarities of diet have often given rise to the assumption that severe interspecific competition is occurring for the various food items. Detailed studies of fish feeding relationships have usually revealed that although the same food items may be taken by different species, the items are taken from different parts of the habitat (Swynnerton and Worthington, 1940; Smith, 1947; Dineen, 1951; Muller, 1954; Carlander, 1955; Gee and Northcote, 1963; Keast, 1965, 1966, 1970; Straskraba et al, 1966), or at different times of the day (Keast and Welsh, 1968), or different species take different-sized individuals of the same prey items (Daiber, 1956; Hopkins, 1965; Keast, 1965, 1966, 1970). Furthermore, overlap in diets has usually been found to be most prevalent in situations of food abundance, whereas food segregation occurs under conditions of food shortage (Shoryghin, 1946b; Keast, 1965; Nilsson, 1965; Zaret and Rand, 1971), so that direct interspecific competition for food may be a seasonal phenomenon.

Within a community, different species are usually specialized for different roles, although many species retain considerable plasticity in their feeding habits. Specialization may be reflected in such things as the general habit (Maitland, 1965), general body form and mouth morphology (Keast, 1965, 1970; Keast and Webb, 1966), structure of the alimentary tract (Nikolsky, 1937; Das and Moitra, 1956a, b), nature of the gills and gill rakers (Das and Moitra, 1956b; Sukumaran et al, 1970), or differences in the relative importance of the various sensory modalities (see Chapter VI). Selection of preferred foods may also be important in reducing competitive encounters (Idyll, 1942; Smith, 1947; Scidmore and Woods, 1959). In this respect, Bryan and Larkin (1972) showed that individual fish may have characteristic food preferences. Within a species, diets may change seasonally and with increase in size (see Chapter VI) and in some species, e.g. perch, Perca fluviatilis; pike, Esox lucius and the white sucker, Catostomus commersonii, the change in diet with increase in size is reflected in structural changes in the alimentary tract (Smyly, 1952; Frost, 1954; Hynes, 1970a).

Keast (1968) found that, in some Ontario lakes, species food

specializations were suppressed at low temperatures. However, he considered that there was probably no increase in interspecific competition at temperatures approaching zero because of the relatively low metabolic requirements of the fish.

In an investigation into the trophic interrelationships of littoral communities of Lake Nyassa, Fryer (1959) found that many of the fish showed preferences for certain food items and that these preferences were accentuated by different distributions within the lake. However, he also found that several closely related herbivorous species coexisted in the same microhabitat and utilized the same foods. He suggested that this situation was possible because of a superabundance of the algal foods on which these species feed. Similarly, Northcote (1954) found that two closely related species of cottids, Cottus asper and Cottus rhotheus, inhabited the upper littoral zones of the same lakes and utilized primarily the same food resources. No information was available on the relative abundance of the food resources and Northcote (loc. cit.) suggested that diversity of habitat in the littoral zone, even in the presence of competition for food, may permit indefinite occupation of the lakes by the two species. On the other hand, Thomerson and Wooldridge (1970), working on the feeding habits of the topminnows, Fundulus olivaceus and Fundulus notatus, suggested that the mosaic distribution of the two species, rareness of sympatry and the prevalence of F. notatus in sympatric populations may be attributed to competitive exclusion between species with similar food niches.

Shoryghin (1946a) considered that interspecific competition for food could be estimated quantitatively from a knowledge of the diets of the fish concerned and the ratio between the availability of food and the amounts required by both competitors. He concluded, within each community, that in species of large population size intraspecific competition was greater than interspecific competition, whilst intra-specific competition in species of small population size was also greater than interspecific competition with other species of small population size, but in some instances it was less than interspecific competition with species of large population size. From investigations into the feeding relationships within fish communities, Frost (1946), Starrett (1950),

Thomas (1962), Maitland (1965), Keast (1965, 1966, 1970) and Straskraba et al (1966) concluded that although competition for food may be possible between any two fish species, because they feed on the same food items, there is little evidence that direct competition for food does in fact occur.

Hynes (1970a) suggested that similarity of diet in two species coexisting in the same habitat indicates that "however else they may be competing, they are not competing for food". This is an over-simplification, since, as pointed out by Chapman (1966), utilization of a food item by one species must have some impact on its availability to another species, even though the two species may occupy different microhabitats. This point has been demonstrated in experimental situations by Brocksen, Davis and Warren (1968) working with the bottom-foraging reticulate sculpin, Cottus perplexus, and the mainly drift-feeding cutthroat trout, Salmo clarki. It was found that the sculpins competed directly with each other and were able to influence the food consumption and production of the trout by cropping the benthic food organisms directly, thereby reducing the number of potential drifting organisms. The trout affected the production of the sculpins very little because their consumption of drifting organisms did not usually materially reduce the benthic populations of food organisms in the laboratory stream tanks. Presumably, if the supply of drifting organisms of benthic origin was drastically reduced in a natural situation, the trout would turn to other food sources, such as fish and terrestrial insects. In a similar series of experiments, Davis and Warren (1965) found that interspecific competition occurred between C. perplexus and the stonefly naiad Acroneuria pacifica. The stonefly naiads were able to crop the common food resource more efficiently than could the sculpins, so that the presence of the stoneflies in the laboratory stream tanks reduced both the food consumption and the production of the sculpins.

It can be assumed that interspecific competition is occurring when the diet of a species changes in the presence of another species (Ivlev, 1961). Such changes were found by Kawanabe (1959) in his studies on food competition amongst river-dwelling fish in Japan. The rivers he investigated contained over 40 species of fish, of which

the most important were the Ayu, Plecoglossus altivelis, cyprinids (Pseudogobio, Tribolodon, Zacco and Carassius), loaches (Cobitis) and gobies (Rhinogobius and Chaenogobius). The Ayu feeds on algae whilst the other species feed on invertebrates and algae. It was found that the free-swimming cyprinids ate more surface food, in the form of terrestrial insects, when the Ayu was abundant and more algae when the Ayu was scarce. The diets of the gobies, loaches and crucian carp also varied according to the presence or absence of the bottom-dwelling cyprinids.

Nilsson (1955, 1957, 1960, 1961, 1963, 1964, 1965), in an intensive study of feeding relationships in Scandinavian lakes, found that trout (Salmo) and char (Salvelinus) showed great similarities in feeding habits when living in separate populations, but generally had dissimilar feeding habits when coexisting in the same lake. However, within the same lake, they had similar feeding habits when food was abundant, but showed a tendency towards greater segregation when food was at a low level. Also, it was found that the introduction of char into previously pure trout-lakes resulted in a decrease in the growth rate of trout. Similar food segregation was also found to occur between whitefish, Coregonus spp. (Nilsson, 1958; Lindstrom and Nilsson, 1962). Nilsson (1965) suggested that the food segregation found in sympatric populations of trout and char and also in different species of whitefish was a result of the exploitation of common resources and interference. Small differences in food preference were thought to be magnified during times of short supply by a combination of innate preference and conditioning.

Andrusak and Northcote (1970, 1971) found a similar situation occurring between lake-dwelling cutthroat trout, Salmo clarki and Dolly Varden, Salvelinus malma. When coexisting in the same lake, both species had more restricted feeding habits and spatial distributions than when living allopatrically. Schutz and Northcote (1972) suggested that different mechanisms of feeding were inherent in sympatric stocks of cutthroat trout and Dolly Varden. They found, experimentally, that different feeding mechanisms were fully expressed in solitary fish and were not magnified by interaction: Dolly Varden fed more successfully

on benthic organisms, whereas cutthroat trout fed more successfully at the water surface. They therefore suggested that segregation was largely selective rather than interactive, but pointed out that both species retained considerable plasticity in their feeding habits.

Rogers (1968), working on the feeding relationships of lake-dwelling threespine sticklebacks, Gasterosteus aculeatus, and the fry of sockeye salmon, O. nerka, found that since the nutritional needs of both species were similar, potential competition for food existed. In localities where there was an unfavourable abundance ratio of fish to food, the growth rate of both species was reduced, even though there were inherent differences in their feeding habits.

A number of workers (e.g. Newman, 1956; McPhee, 1961; Magnuson, 1962; Nilsson, 1963, 1965) have shown that aggression is often associated with feeding and that aggression appears to be reduced in conditions of food abundance. Salmonids also appear to be able to tolerate contemporaries at closer range if food is abundant (Chapman, 1966). As pointed out by Nilsson (1967b), feeding actions could easily be transformed into aggressive behaviour. He cites the observation of Kalleberg (1958) that the frontal threat display of young salmonids is very similar to their behaviour when swimming towards a prey item on the bottom. Magnuson (loc. cit.), working with medaka, Oryzias latipes, concluded that aggressive behaviour was not used in competition for space as such, but rather was a mechanism which reserved a greater portion of a limited food supply.

The introduction of a species into new areas provides opportunities to examine competitive feeding interactions, particularly if conditions are known prior to the introductions (Nilsson, 1967b). For example, analysis of the events following the introduction of the redside shiner, Richardsonius balteatus, into a Canadian lake containing rainbow trout, Salmo gairdneri, indicated that although competition for food occurred between the two species, it was part of a complex of interactions which also included mutual predation (Larkin and Smith, 1954; Crossman, 1959; Johannes and Larkin, 1961).

In conclusion, it can be said that probably in the majority of instances severe interspecific competition for food is discontinous and

is probably "restricted to more or less acute convergence of requirements for a resource for limited periods" (Weatherley, 1972). As suggested by Hartley (1948), who concluded that most of the generalized feeders in fish communities are facultative, the tendency to readily change the relative proportions of dietary constituents is perhaps the major method by which fish avoid direct competition for food. Indeed, the generalized feeding habits of fish may be regarded as an important factor in maintaining the stability of fish communities (Pliszka, 1953).

(2) Feeding relationships of the fish in the River Glentui

As pointed out in Chapter VI, the same food organisms were generally utilized by all fish species in the River Glentui, with larvae of Deleatidium spp. forming the major part of the diet of all fish except the eels. However, the relative proportions of the various items in the diet varied between species. Kendall rank correlation coefficients for comparisons of the species diets assessed by the points method (Table 38) indicated that the diets of the native species were dissimilar, with the exception of the diets of G. vulgaris and P. breviceps in May, but that the diet of the introduced brown trout, in six out of nine instances, was similar to the diets of the native species.

Although G. vulgaris and P. breviceps, the two most numerous species in the River, take food items of the same size range, evidence suggests that G. vulgaris feeds on drift, whilst P. breviceps is primarily a bottom-feeder (see sections 7. and 8. in Chapter VI). Different feeding periodicities (see section 7.(2) (b) in Chapter VI) and the spatial distribution of the two species (see section 1. of this Chapter) may further reduce direct feeding encounters. Different spawning times also ensure that there is no large overlap of young G. vulgaris and P. breviceps feeding in the quiet parts of the River. The eels, which are capable of feeding on a much wider size-range of items than either G. vulgaris or P. breviceps, feed mainly by means of olfaction and normally feed only at night. Trout smaller than 20 cm in length were normally found in the same microhabitat as adult G. vulgaris, whereas trout larger than 20 cm long occurred in the deeper channels and pools. Trout are primarily visual drift feeders and since G. vulgaris obtains its food in a similar manner, it is likely that interspecific encounters between the two species

may occur when feeding. The gape of the large fish (the largest trout taken in the present study was 31 cm long) also enables S. trutta to take food items which in its absence would be available only to the eels.

The fact that different species feed on the same organisms does not of itself indicate that interspecific competition for food is severe. However, by definition (see beginning of this Chapter) any species which eats the same food as another species is potentially limiting the food supply to that species and is therefore competing with it for food. In nature, the severity of this competition is modified by a number of factors and is often reduced by the generalized feeding habits of fish (see previous section). The larvae of Deleatidium spp. formed a substantial part of the diets of G. vulgaris, P. breviceps and S. trutta during the present study period and it may be concluded that the larvae of this ephemeropteran are capable of maintaining high densities despite heavy predation. If competition for Deleatidium becomes severe, either directly (by two fish of different species attempting to take the same item from the drift) or indirectly (because one species limits the supply to another by cropping Deleatidium directly off the substrate), then presumably there will be a shift in the diets of the competing species. Intraspecific competition for food is probably severe in recently-hatched G. vulgaris and P. breviceps which occur in large numbers in the quieter parts of the River. Brown trout become territorial soon after leaving the redd (Kalleberg, 1958) and both adult G. vulgaris and P. breviceps possess intraspecific behavioural mechanisms which cause individuals to be spatially segregated, so that direct competition for food is reduced. Interspecific competition for space appears to occur between G. vulgaris and P. breviceps, so that differences in distribution within the River may reduce direct interspecific competition for food. The same situation may also apply between G. vulgaris and certain size-groups of S. trutta, but direct competition for food between these two species, both of which feed on drift and have similar activity patterns, is probably more acute than between any other pair of species in the River Glentui. The situation between G. vulgaris and S. trutta is not comparable with that described by Fryer (1959) for lake Nyassa, in which a number of herbivorous fish coexisted in the same microhabitat

and ate the same food. In the lake situation, food was continually plentiful, whereas stream drift tends to be periodic in its abundance, occurring mainly at night in the River Glentui.

Brown trout were not abundant in the River Glentui, even though the River is relatively stable (see Chapter I). They are frequently salvaged from isolated shallow pools in the River Ashley during periods of drought (North Canterbury Acclimatization Society, pers. comm.), so that it is likely that high mortality of adult fish in the River Ashley may result in reduced spawning in tributaries such as the Glentui. Since G. vulgaris is relatively abundant in the River Glentui (see Table 26), the degree of competition between adult G. vulgaris and S. trutta in riffle areas would tend to be greater than intraspecific competition between individual S. trutta (see Shoryghin, 1946a).

Philypnodon breviceps was the only species in the River Glentui which did not utilize one of the other fish species as a food source, although it did exhibit cannibalism. Galaxias vulgaris and S. trutta were found to take P. breviceps on rare occasions, whilst trout, galaxiids and bullies formed a substantial part of the diet of the eels, on a points basis (see Figs. 38, 39 and 40).

In summary, all fish species utilized the invertebrate fauna and exhibited varying degrees of overlap in their diets, although direct competition for food was probably only severe between G. vulgaris and S. trutta. Eels preyed upon the other three fish species present.

Chapter VIII

GENERAL DISCUSSION - A REASSESSMENT OF THE RELATIONSHIPS BETWEEN THE INTRODUCED BROWN TROUT AND THE NATIVE FRESHWATER FISH FAUNA, PARTICULARLY THE GALAXIIDAE

Seven species of salmonids have been successfully introduced into New Zealand (Hopkins and McDowall, 1970). Salmo trutta was first introduced in 1867 and by the end of the century the stocks were very similar in abundance and distribution to those found today (Stokell, 1955; Allen, 1956; Lamb, 1966). The effects of both the accidental and deliberate introduction of fish species into new areas has been documented by a number of workers (see, e.g. Gause, 1934; Curtis, 1942; Hazzard, 1946; Bump, 1951; Fenderson, 1954; Dymond, 1955; Miller, 1960; Brynildson et al, 1964; Myers, 1965; Nelson, 1965; Nilsson, 1967b; McDowall, 1968c; Smith, 1970) and the ecology of introductions in general has been discussed by Hobbs (1955), Elton (1958) and Mayr (1965). Thomson (1922) remarked that competition with the introduced species for the same resources appears to have been partly responsible for the disappearance of some native species of fish in New Zealand, but he pointed out that it was difficult to separate the effects of competition from the undoubted effects of introduced predators and the disturbance of habitats by man. Allen (1961) considered that the native fish were not adversely affected to any great extent by the introduced salmonids. However, Fish (1966) found that the disappearance of a galaxiid (unidentified) from a small Northland lake followed the introduction of S. gairdneri. McDowall (1968b) in a review of the problems of fish introductions and the interactions of the native and alien faunas of New Zealand, concluded that although data were not conclusive throughout New Zealand that trout are detrimental to stocks of native fish and other aquatics, "it is clear that in some localities and for some species, there has been extinction or marked stock reduction of native forms associated with the presence of the introduced trout."

Phillips (1929), Percival (1932), Cairns (1942), Allen (1951)

and Lane (1964) have indicated that, since the diets of trout and native fish overlap, competition for food may occur. Burnet (1963, 1969a) found that although the diets of eels (A. dieffenbachii and A. australis) and S. trutta overlapped to some extent, there were major differences which suggested that there was little competition for food. In the stream in which he worked, there was evidence that the eels and trout fed in different areas, with the trout food originating from the fauna of gravel areas, whilst the eels utilized the fauna of weed beds, most of which was not available either directly or indirectly (as drift) to the trout. However the feeding relationships of eels and trout probably vary between one body of water and another, depending on local conditions.

Trout have been found to feed on small galaxiids, eleotrids and retropinnids (Phillipps, 1924; Allen, 1961; Percival and Burnet, 1963), whilst trout themselves may be taken by eels (Cairns, 1942; Burnet, 1952). Much attention has been given to the relationship between eels and trout, since because their food demands overlap and eels may prey upon trout, eels are considered to be detrimental to the trout fishery. From a study of trout populations in eel-less waters, Cairns (loc. cit.) suggested that the absence of eels may be of great benefit to trout stocks. Burnet (1959, 1968) examined the effects of removal of eels from trout waters and considered that the effects of removal depended on the character of the river and the relative abundance of each species. In a situation in which the eel population was relatively large compared with the trout population, removal of eels resulted in an increase in trout numbers, but this was correlated with a reduced growth rate and a decline in the condition of the trout.

Hopkins (1965, 1970) studied the feeding relationships of P. breviceps, S. trutta fry, A. dieffenbachii and A. australis in two small streams and found that there was considerable overlap in the diets of the four species, particularly with respect to the larva of Deleatidium. However, it was noticed that the trout fry, bullies and eels preferred a different size range of Deleatidium, the trout taking the smallest and the eels the largest larvae, whilst "the very young larvae which formed the bulk of the Deleatidium population were largely

untouched." It was suggested that the food requirements of the similar-sized trout fry and juvenile P. breviceps were sufficiently alike to modify the diet of the two species. Hopkins (1965) concluded that although all four species were exploiting the same food organisms, "their various preferences were such as to avoid serious competition." Even though the number of interspecific encounters may have been reduced by each species feeding on different-sized prey organisms and by feeding in different microhabitats, the fact remains that since S. trutta was feeding on the smaller-sized Deleatidium larvae it was potentially limiting the supply of larger larvae to the other species. It is significant that in these study streams, Galaxias divergens was abundant only in one locality which, because of waterfalls, was relatively inaccessible to trout (Hopkins, 1971b).

McDowall (1968b) pointed out that some species of galaxiids particularly G. divergens, G. vulgaris, G. paucispondylus, G. fasciatus, G. argenteus and G. brevipinnis do not appear to be compatible with trout. In this respect, he suggested that competitive displacement seems more likely to be important than predation, particularly in the case of small trout. As in G. vulgaris, G. divergens appears to obtain at least part of its food requirements from stream drift (Hopkins, 1971a). The natural feeding habits of the other galaxiids mentioned above are unknown, although Eldon (1969) has observed the behaviour of some of them in aquaria: G. fasciatus is adept at taking insects from or just above the surface of the water, whilst both G. argenteus and G. brevipinnis take food from all levels of the water column. Their dorsal brain patterns suggest that vision plays an important role in the ecology of these galaxiids (see section 9.(5) of Chapter VI). The feeding behaviour of these fish is very similar to that of S. trutta. All are carnivorous, indeed there are no native herbivorous fish in New Zealand (McDowall, 1970). Since their food requirements and feeding mechanisms are similar, direct interspecific competition for food is likely to be severe between S. trutta and the above mentioned galaxiids. In addition, indirect competition will occur because since their food requirements are similar one species will potentially limit the supply to the other. Interspecific aggression whilst feeding (see section 3.(1) of Chapter VII) probably also accentuates the effects of competition for food.

Similarly, in Australia, Frankenberg (1966) reported that introduced trout appeared to have fragmented the range of galaxiids into a number of small isolated populations. In one river, it was found that S. trutta occupied the main body of the river, whilst galaxiids were only found in situations inaccessible to trout, such as above waterfalls. Also, in a small high-altitude lake, S. trutta appears to have replaced Galaxias coxii, a primarily visual feeder which readily takes insects from the water surface and has been observed taking insects flying above the water (Walford, 1928).

It is suggested that the relationship between G. vulgaris and S. trutta in the River Glentui may explain the incompatibility of other galaxiids and S. trutta. Although predation on galaxiids by the larger trout may occur, it seems that direct competition for food, combined with interspecific aggression and similar microhabitat requirements, is responsible for the reduction in abundance of galaxiids in areas occupied by S. trutta. As pointed out by McDowall (1968b), the situation in New Zealand appears to be similar to that described by Miller (1960) for the American south west, where "under natural conditions there was a low saturation fauna of freshwater fishes with little interspecific competition and little predator pressure. These fishes were therefore susceptible to competitive displacement and stock decline when habitat analogues and predators were introduced, leading in some cases to extinction."

Further experimental analysis of the spatial and feeding relationships of S. trutta and "incompatible" galaxiids would be a fruitful line of research in the understanding of competitive interactions. In this respect, the use of large-scale stream tanks and/or controlled sections of natural waterways is to be recommended. However, before such work could be attempted with most galaxiids, more basic information on their life histories is required (see final discussion in Chapter IV). The adult brain patterns of the New Zealand members of the Galaxiidae, although organized on the same basic plan, show a wide variation in the proportions of the dorsal aspects of the forebrain, optic lobes and cerebellum, indicating the probability of vastly different ways of life (see section 9. of Chapter VI). Therefore, competitive intensity

may be expected to differ between S. trutta and the various members of the family, depending on the degree of similarity in ecological requirements. Also, once basic life history patterns are known, interspecific relationships at the various stages may be assessed. Intraspecific size-related changes in galaxiid dorsal brain patterns indicate that juvenile and adult fish may lead completely different ways of life, so that interspecific relationships may change at the various life history stages and may include mutual predation as well as competitive interactions.

Chapter IX

SUMMARY

1. This study is concerned with aspects of the ecology of G. vulgaris in the River Glentui, Canterbury, New Zealand.

2. Fish were aged by means of sagittal otoliths and length frequency analysis. Most G. vulgaris were found to belong to the age groups 0+, 1+ and 2+, a few were in the 3+ and 4+ age groups, none were found in the 5+ age group, and one was found in the 6+ age group, in its seventh year.

3. Annual growth in length was estimated by back-calculation from otoliths. Length achieved at the end of the first year of life was not significantly different between males and females. However, after the first year, growth in length of males lagged behind that of females. The von Bertalanffy equation adequately described annual growth in length of both males and females.

4. Seasonal growth in length was estimated from monthly changes in the mean length of each age group. Increase in length of both males and females occurred from November through to May, whilst growth ceased from June to October, in winter and early spring. Differences in growth in length were apparent between year classes and between fish sampled in different parts of the River.

5. Growth curves, describing seasonal growth in weight of the younger age groups, were fitted using mean wet weights of each age group. Possible factors affecting the growth of G. vulgaris were discussed.

6. The length:weight relationship was calculated separately for males and females and for age 0+ and older fish of each sex. Since the b coefficient for each group differed significantly between bimonthly samples, changes in coefficient a could not be used to compare condition at various times of the year. Changes in condition therefore were considered in terms of predicted weight values for hypothetical fish using the bimonthly regression coefficients calculated for each group. The condition of age 0+ fish increased throughout the growing season.

In older fish, both males and females, there was an increase in condition in late spring and autumn and a reduction in condition in early spring and summer. Females were generally in better condition than males. Somatic tissue was found to undergo seasonal changes, irrespective of gonad development. The seasonal changes were reflected in the fat deposits overlying the alimentary tract.

7. Monthly gonosomatic ratios and gonad condition indicated that spawning occurred in late winter and early spring. The annual maturation cycle of oocytes, as indicated by length frequency analysis, was described. Many males spawned in their first year of life, whereas no females spawned until their second year.

8. Fecundity varied between 284 - 1,911 eggs per female. The regression equations describing the relationship of fecundity to fish length, weight and age were presented. Weight was found to be the most important factor influencing fecundity.

9. The relationship between maturity, size and age was discussed. In males, the attainment of maturity was found to depend on size, whereas in females age appeared to be the most important factor.

10. The total sex ratio was 1:1. However, the sex ratio of potential spawning fish indicated that more males than females took part in the spawning process.

11. The spawning area, nest site, characteristics of the egg mass and behaviour during the spawning season were described. The excavation of nests was performed primarily by males. Evidence suggested that at each spawning, a female sheds all her eggs, whereas males do not shed all their sperm. Males showed greater attachment to the nest site than females. Field observations suggested that temperature played an important role in the initiation of spawning.

12. Field and laboratory evidence indicated that recently-hatched fish are swept downstream after hatching and complete their early growth in the quieter parts of the River, not in the normal adult riffle habitat.

13. The mechanism of spawning, which showed a number of similarities to that of S. salar, was discussed. It was considered that age 0+ males act as a form of insurance by increasing the proportion of potential spawning males, thereby ensuring that all eggs are fertilized.

14. It was suggested that the presence of fewer and larger eggs in G. vulgaris, compared with the diadromous species such as G. maculatus, is the result of a more precise fertilization process, with subsequent survival of more fertilized eggs.

15. A mark and recapture experiment carried out over a period of 11 months indicated that G. vulgaris occupies a restricted home range. Movement to suitable adjacent areas was found to occur if the original area became unsuitable. An upstream spawning movement may take G. vulgaris temporarily out of its home range. Possible factors affecting the upstream movement are discussed.

16. Homing in stream fish and its sensory basis was briefly discussed. Two experiments in which G. vulgaris was artificially displaced indicated that downstream-displaced fish were less disorientated than upstream-displaced fish. It was suggested that displaced fish responded to an overall stimulus, probably chemical in nature and olfactorily mediated, in locating their home range. The findings of the experiments were discussed in relation to the results obtained by other workers.

17. Laboratory evidence suggested that movement of juvenile fish to the adult riffle habitat takes place in an upstream direction.

18. Population estimates based on the results of the mark-recapture experiment indicated that there were between 0.4 - 0.6 G. vulgaris/m^2 in the sampling sections.

19. The basic food of G. vulgaris consisted of the larvae of Deleatidium spp., Coloburiscus humeralis and Nesameletus sp.; secondary foods included terrestrial arthropods, elmids and the larvae of Hydrobiosis sp., Hydropsyche colonica, Archichauliodes diversus, Olinga sp., Pycnocentrodes sp., chironomids and simuliids. The diet was discussed in relation to season, age, size and sex. Food consumption appeared to be greatest in spring and summer.

20. Measurement of the spontaneous locomotory activity of G. vulgaris indicated that it is nocturnal for most of the year, except for a short period during the spawning season. Feeding was found to be dependent on activity.

21. The diets of P. breviceps, S. trutta and Anguilla spp. in the River were discussed. A comparison of the diets of all species indicated that in general they utilized the same food organisms, although the relative proportions of the various items differed between species. Eels preyed upon the other fish species present.

22. The relationship between the invertebrate drift fauna and the feeding habits of G. vulgaris and P. breviceps over a 24-hour period was analysed. Drift patterns of the major drifting organisms were presented. Light intensity appeared to be the major factor controlling the periodicity of the night-active forms, whilst the occurrence in the drift of the day-active forms was correlated with water temperature. Galaxias vulgaris had two peaks of feeding during the night. Philypnodon breviceps also had two peaks, which occurred at midnight and midday, between the peak feeding times of G. vulgaris. In a number of instances, the feeding of G. vulgaris on its major food items coincided with a period of abundance of the item in the drift, whereas the feeding of P. breviceps was not positively associated with the occurrence of the food item in the drift.

23. The feeding mechanisms of the fish species in the River were discussed. Galaxias vulgaris and S. trutta were considered to be primarily visual drift feeders; P. breviceps was considered to be a bottom-feeder in which vision and taste play important roles in the location and capture of food, whilst the nocturnal Anguilla spp. were considered to rely primarily on olfaction.

24. Size-related changes in the relative proportions of the dorsal aspects of the forebrain, optic lobes and cerebellum in G. vulgaris were described and were related to the change from the free-swimming, open-water existence of the juveniles, which inhabit the quiet stretches of the River, to the cryptic way of life of the riffle-dwelling adults.

25. The dorsal brain patterns of juvenile and adult G. vulgaris, G. maculatus and N. burrowsius were compared. The juveniles of each species lead a similar open-water existence and have similar dorsal brain patterns. The open-living existence persists in adult G. maculatus which retain the juvenile-type brain pattern. The cryptic habits of adult G. vulgaris and, more particularly, N. burrowsius are reflected

in changed dorsal brain patterns.

26. The dorsal brain patterns of the New Zealand Galaxiidae were compared in an attempt to elucidate the ecology of the lesser known species.

27. The distribution of the fish species in the River was discussed. Stream tank experiments to examine the effects of competition for space between G. vulgaris and P. breviceps and between G. vulgaris and S. trutta were described. The results suggested that interactive segregation occurs between G. vulgaris and P. breviceps. Also, competitive interactions may occur between adult G. vulgaris and certain size groups of S. trutta. It was considered that interspecific competition for spawning sites did not occur in the River.

28. Feeding relationships of fish at the same trophic level were discussed. Any species which feeds on the same food item as another species is potentially limiting the food supply to the other species and is therefore, by definition, competing with it for food. A number of mechanisms reduce direct food competition. In nature, severe competition for food is probably discontinuous and restricted to an acute convergence of requirements for limited periods.

29. Different feeding mechanisms, spatial distribution, feeding chronology and utilization of different-sized food organisms reduce direct competition for food between the native species of fish in the River Glentui. However, the feeding mechanisms, spatial distribution and activity cycles of adult G. vulgaris and certain size-groups of S. trutta were similar, suggesting that direct competition for food between the two species may be severe.

30. The effects of the introduced S. trutta on the native freshwater fish fauna were discussed, with particular emphasis on the relationship between brown trout and the Galaxiidae. It was suggested that the similar food requirements, feeding mechanisms and habitat preferences of trout and galaxiids are responsible for the reduction in abundance of certain galaxiids in areas occupied by S. trutta.

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Appendix 1

THE CANTERBURY MUDFISH - NEOCHANNA BURROWSIUS

The taxonomy of N. burrowsius, a fish which was not described until 1926 (Phillipps, 1926), was recently reviewed by McDowall (1969b, 1970). Very little is known of its ecology. Skrzynski (1968) summarized all the available information and concluded that the species is now almost extinct. He discussed possible reasons for its decline and considered that changes in the vegetation-climate pattern and, more particularly, recent drastic changes of the environment by man were responsible for the decline. It was originally intended that the ecology of this endangered species would be the subject of the present thesis. However, preliminary investigations indicated the unsuitability of N. burrowsius as a study animal, the major difficulty being the inability to find a sufficiently large population on which to work. The information gained in the preliminary investigations on the ecology and distribution of N. burrowsius is presented here.

1. Distribution and Habitat

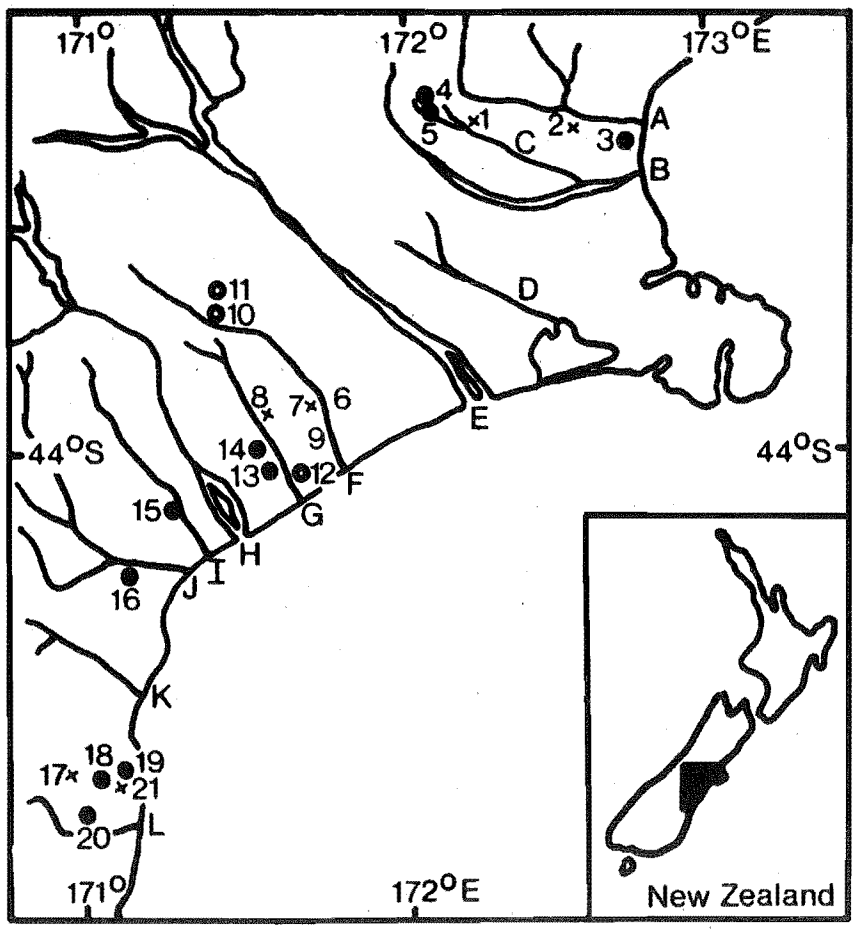
Attempts were made to find N. burrowsius at sites where it had previously been recorded. New sites were discovered mainly from replies received in response to circulars sent to people likely to encounter the mudfish, e.g. drain-clearers and farmers. Electric fishing and hand-netting were used in combination when searching for fish.

Localities at which N. burrowsius has been found are presented in Fig. 1. Details of habitat type and the status of the species at each site are presented in Table 1. It may be seen that no mudfish were found in many of the localities at which they were previously recorded and that, in most instances, mudfish were found in man-made or man-modified habitats. Only small numbers of fish (usually less than 10 individuals) were found at each site. However, at locality No. 10, 46 fish were recorded on one occasion, most of which were returned to the site. The small numbers of fish taken at each locality probably reflect, to some extent, the inadequacy of the collecting technique, because since mudfish were generally found in overgrown drains and irrigation races, it was often difficult to see the fish once they had been stunned.

FIGURE 1. Localities at which N. burrowsius has been found: the area covered by the map is shown in the inset of New Zealand.

Localities are numbered 1 – 21; details of each site are presented in Table 1; x = mudfish found at these sites before 1968, but not found here during the present investigation; o = mudfish found at these sites before 1968 and again during the present investigation; ● = new mudfish localities recorded in the present investigation; 6, 9 = mudfish localities whose precise locations were not recorded by previous investigators. The rivers marked on the map are:

A. Ashley
B. Waimakariri
C. Eyre
D. Selwyn
E. Rakaia
F. Ashburton
G. Hinds
H. Rangitata
I. Orari
J. Opihi
K. Pareora
L. Waihao


171°
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I
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16
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17×
18
19
21
20
L
171°
172°E
44°S
New Zealand

TABLE 1 Details of localities at which *N. burrowsius* has been found: the locality reference numbers (Ref.) refer to the localities shown in Fig. 1. (E = mudfish not found at these sites during the present investigation; P = mudfish found at these sites during the present investigation; Sk1 – Sk9 refer to the collection numbers quoted in Table 1 of Skrzynski's (1968) paper; map references refer to N.Z.M.S. 1 (1:63,630) published by the N.Z. Department of Lands and Survey)

Ref.	Name	Mudfish Status	Remarks
1	West Oxford	E	Sk1; recorded by Phillipps (1926); mudfish originally found in a creek which periodically dried up; whole area has since been drained.
2	near Rangiora	E	Sk4; recorded by Stokell (1949); mudfish found in drain which periodically dried up. No water has been in the drain for the last three years.
3	Woodend	P	mudfish found in swamps which were in the process of being drained, and also in flooded pasture at the margins of the swamps.
4	Coopers Creek	P	mudfish found in pond formed by the blocking of an irrigation race.
5	Coopers Creek	P	mudfish found in pools which formed the remains of an irrigation race which periodically dries up.
6	near Ashburton	–	Sk2; recorded by Stokell (1938); precise locality and habitat type not recorded.
7	near Tinwald	E	Sk3; recorded by Stokell (1945); mudfish originally found in a small creek which has recently become part of an extensive irrigation system.
8	River Hinds	E	Sk6; recorded by Lane (1964); mudfish originally found in a small pool below a fall in the Valetta irrigation race near where it enters the River Hinds (map S92, ref. 015 113). They were probably swept into the race from smaller ditches further upstream (Lane and Skrzynski, 1972); subsequent fishings have yielded no further mudfish.
9	near Tinwald	–	Sk7; recorded by Woods (see Skrzynski, 1968) in the overgrown backwaters of a drain; precise locality not recorded.
10	Anama	P	Sk8a, 8b; originally recorded by Fisheries Research Division (N.Z.M.A.F.) personnel; mudfish found in the remains of a filled-in stock race; map S91, ref. 907 295.

11	Gawler Downs	P	Sk9; originally recorded by Fisheries Research Division (N.Z.M.A.F.) personnel; mudfish found in an overgrown stream with a mud bottom and very little flow; map S81, ref. 835 375.
12	Eiffelton	P	Sk5; mudfish found in small (0.6m wide,<0.4m deep) muddy drain (see Skrzynski, 1968).
13	Flemington	P	mudfish found in small muddy drain.
14	Hinds	P	mudfish found in an isolated part of a drain.
15	Geraldine	P	mudfish found in Te Moana stream (Hurley, pers. comm.), probably from an irrigation race.
16	Temuka	P	map S111, ref. 744 616; mudfish found in an irrigation race.
17	Waituna	E	mudfish found originally in 1930's in a pond overgrown with weed (W. I. Ross, pers. comm.). The pond has since been filled in and the whole area drained.
18	Waimate	P	mudfish found in one of a series of ponds which formed the remains of a dried-up water course (originally recorded by B. Vincent (N.Z. Department of Internal Affairs) - Eldon, pers. comm.); map S119, ref. 612 122.
19	Willowbridge	E	mudfish found in a shallow muddy pond and in the stream flowing into it; found by Stokell (Keillor (Waitaki Valley Acclimatization Society), pers. comm.); map S128, ref. 675 052; the pond was dry when visited during the present investigation and no mudfish were found: it is, however, subject to periodic flooding and would appear to be a suitable mudfish habitat.
20	Ikawai	P	mudfish found in an artificial waterhole (1.5m diameter,<0.5m deep) approximately 0.5km from a swamp: no mudfish were found in the swamp; map S127, ref. 475 926; mudfish were also found in a small drain in the same area.
21	Waimate	E	mudfish found in an artificial water hole (Keillor, pers. comm.); map S119, ref. 665 122. Keillor (pers. comm.) has also received specimens of N. burrowsius from a number of other localities, mostly artificial (e.g. flood water drains, irrigation races), in the Waimate region.

Both Phillipps (1926, 1940) and Stokell (1949, 1955) reported the ability of N. burrowsius to survive for several weeks in damp earth. Phillipps (1926) cited a personal communication describing the finding of N. burrowsius in a waterhole which had become dry ..... "on digging the bank down I found in it holes shaped like a coconut in which the fish hid, each with a small entrance. The holes were very smooth inside, and could hold water for a long time if the entrance was carefully closed from the inside." Observations made during the present study indicate that N. burrowsius may occupy similar holes under non-drought conditions. In three instances, small, smooth-walled chambers, each with a tunnel to the surface, were found in mud-banks at or just above the water level in laboratory aquaria. Each chamber contained a mudfish: the dimensions of one containing a mudfish 81 mm long were as follows:

length of tunnel from surface of mud to chamber = 3.4 cm
diameter of tunnel entrance at surface of mud = 0.9 cm
greatest length of chamber = 5.7 cm
depth of chamber at its midpoint = 1.6 cm
width of chamber at its midpoint = 1.1 cm

However, in laboratory aquaria, mudfish were generally found curled upon themselves up to 3 cm below the surface of wet mud. It is likely that under drought conditions the fish would be capable of following moisture down holes left by rotted vegetation, as indicated for the brown mudfish, Neochanna apoda, by Davidson (1951), and of maintaining themselves well below the surface of the mud until wet conditions returned. Aestivation was demonstrated in four fish which survived for three months in laboratory aquaria containing initially damp mud which soon dried. The fish did not move when dug out of the mud, but became active immediately on being placed in water. Skrzynski (loc. cit.) considered that N. burrowsius originally occupied isolated bodies of water which periodically dried. The other two neochannoid species, viz. N. apoda (found on the west coast of the South Island and in the south of the North Island of New Zealand) and N. diversus (found in the north of the North Island) are also capable of aestivation (see Gunther, 1867; Roberts, 1872; Phillipps, 1923; Davidson, 1951; Stokell, 1955; McDowall, 1970; Eldon, 1971) and have been found in unmodified areas in forest puddles, bogs and

swamps, and in creeks which are usually filled with rooted vegetation (Eldon, 1968; McDowall, 1970). As pointed out by Skrzynski (loc. cit.), such unmodified waters were once common in the Canterbury region but have now been almost eliminated by man's activities.

2. Food

The feasibility of using emetics to collect stomach contents of N. burrowsius and so avoid killing the fish was investigated using G. vulgaris. The method proved unsuccessful (see Chapter VI).

Lane (1964) examined the stomach contents of five N. burrowsius taken at locality No. 8 and found that they consisted of "99% crustacea". In the present study, the contents of 27 stomachs were analysed, seven of which were empty. The results of the analysis are presented in Table 2.

TABLE 2 Food of N. burrowsius. Figures in body of table refer to numbers of individual food items: P indicates that items were present, but were not counted. Locality numbers refer to the corresponding numbers in Fig. 1 and Table 1. (n = number of stomachs examined; L = larva; A = adult).

	locality No.4 (n = 3)	locality No.10 (n = 13)	locality No.12 (n = 2)	locality No.13 (n = 1)	locality No.18 (n = 1)
Austrosimulium longicorne L.		142			
chironomid L. *		12			
tipulid L.		5			
stratiomyid L.		3			
Xanthocnemis zealandica L.		2			
coleopteran L, A.		2	1		
trichopteran A.		2			
lepidopteran caterpillar		1			
crustaceans	7	61			
lumbricids		5			
N. burrowsius eggs		23	1	1	
invertebrate eggs	P				P
plant material **		P	P	P	

* Orthocladiinae sp. and Tanytarsini sp. (Winterbourn, pers. comm.)

** includes filamentous algae (Spirogyra); diatoms including Synedra, Cocconeis, Navicula and Acnanthes (Flint, pers. comm.) and small pieces of vascular plants.

TABLE 3 Gonad indices of N. burrowsius

$$\left(\text{gonad index} = \frac{\text{gonad weight}}{\text{somatic weight}} \times 100\right)$$

Male					Female				
Month	locality	TL (mm)	wt. (gm)	gonad index	Month	locality	TL (mm)	wt. (gm)	gonad index
Jan.	3	100	4.5	2.30	Feb.	10	54	1.1	0.67
Feb.	10	69	2.3	0.73		10	122	13.9	1.69
	10	63	1.6	1.21	July	10	102	6.9	27.60
	10	106	8.9	1.87	Sept.	10	93	10.7	0.61
March	3	58	0.9	2.74	Oct.	10	89	3.6	0.68
July	10	103	8.4	24.34	Dec.	12	70	1.8	0.43
	10	89	4.5	26.39		12	77	2.3	0.39
	10	78	2.7	13.18		12	78	2.1	0.83
	10	80	2.6	30.96					
Sept.	10	95	5.0	4.76					
Nov.	10	110	8.7	0.62					
	10	106	9.0	0.50					
	10	98	6.7	0.34					

Aquatic insects formed the bulk of the diet, with crustaceans being the next most abundant item, followed by N. burrowsius eggs. Plant material was found in nine stomachs, but it was significant that it occurred only in the samples in which N. burrowsius eggs were recorded. Most of the diatoms were of types which are normally found on the surface of submerged higher plants (Flint, pers. comm.), situations where N. burrowsius eggs are found (see Section 3.). Also, the alimentary canal of N. burrowsius is of the simple carnivore type, i.e. with the intestine running straight from duodenum to anus, as in N. apoda (Davidson, 1949, unpublished) and G. vulgaris. It therefore appears that the plant material was consumed at the same time as the eggs were taken and that it does not form part of the diet of N. burrowsius.

3. Life History

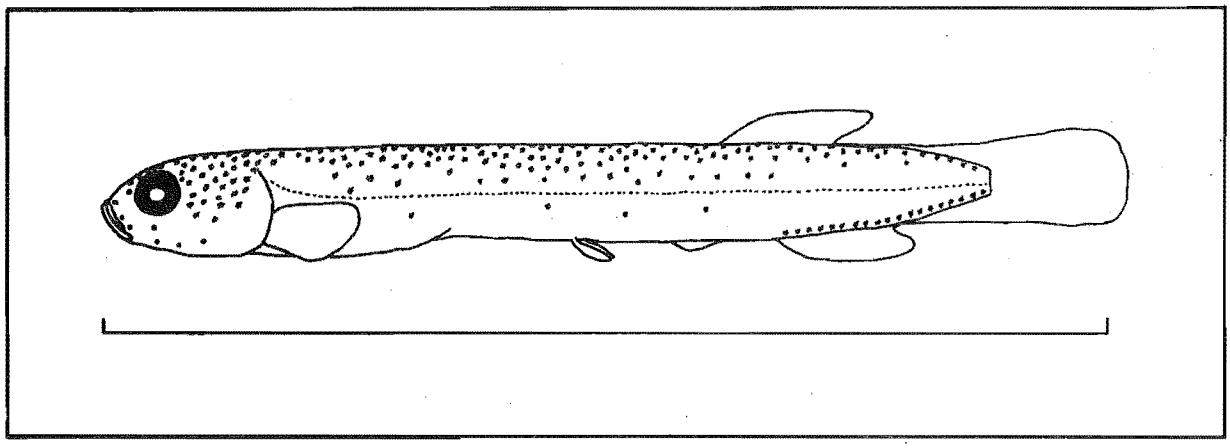
Skrzynski (1968) suggested that N. burrowsius probably spawns in late August or September (late winter - early spring), whilst McDowall (1970) suggested spring as the spawning time. In the present study, gonad indices (see Table 3) were found to be high in July and low in September, and an examination of the N. burrowsius population at locality No. 10 on 24-8-71 and 11-10-71 indicated that spawning had occurred between the two visits: all fish examined in August were ripe, whereas those examined in October were spent. Also, N. burrowsius eggs were found in the guts of mudfish from August to October. Thus, spawning was found to occur in late winter and early spring.

Captive mudfish (two fish of each sex) spawned in an outdoor aquarium in October, after a period of heavy rainfall, the eggs hatching after 23 days (Lake, pers. comm.). The aquarium contained willow roots and the eggs were found singly on the roots, in some instances above the surface of the water. Eldon (1971) discussed the suspected terrestrial deposition of eggs in N. apoda and suggested that the eggs were probably laid and fertilized in the water and then splashed from the water by the action of body and tail. In the natural situation, this would distribute the eggs amongst vegetation and detritus in the shallow pools and swamps in which N. apoda is found. Similar behaviour probably occurs in N. burrowsius, although most of the eggs in the situation described above were found on vegetation below the surface

FIGURE 2. Juvenile N. burrowsius. Scale = 30 mm.

Note : a. distribution of melanophores – mainly on head and along dorsal trunk,

b. small median fin between the anal fin and pelvic fins.



of the water.

Rainfall (or an increase in water level) appears to be a necessary stimulus for the release of spawning in N. burrowsius. Six groups of mudfish failed to spawn in indoor aquaria in which the water levels were constant. The indoor aquaria were generally kept under normal night-day conditions, but the temperature in each was probably higher than in the outdoor aquarium.

That there are differences in the life histories of the three neochannoid species is indicated by the number and size of the eggs in each species. Neochanna apoda and N. diversus have few moderately large eggs, whereas N. burrowsius has many small eggs (see Table 4), comparable to those produced by G. maculatus (see Chapter IV).

TABLE 4 Fecundity of the three neochannoid species. Data for N. apoda and N. diversus are from McDowall (1970). Measurements were made on unshed eggs. (n = sample size).

Species	TL(mm)	No. eggs	Mean diameter of eggs(mm)
N. apoda	115	533	1.75
N. diversus	119	940	1.60*
N. burrowsius	94	1,666	-
	102	1,880	-
	109	2,830	-
	151	10,074	0.67** (n = 1,000)

* these eggs were not ripe: ripe eggs would therefore be larger than this
** eggs measured in female taken in August

Spawning appears to take place in the normal adult habitat. Although no eggs were found (except in the stomachs of other mudfish), spent fish were found at locality No. 10 in October, whereas in August all fish examined at the site were ripe.

Juvenile N. burrowsius (see Fig. 2) were found to be active in the water column during daylight and, in the outdoor aquarium mentioned previously, they were observed to shoal. On the other hand, adults were nocturnal. At locality No. 10, adults were observed by

spotlight resting on the surface of the mud substrate at night: they were never seen during daylight. Measurement of the spontaneous locomotory activity of a mudfish 101 mm long (using the apparatus described in Chapter VI) indicated that it was primarily active at night (diel activity ratio (calculated from mean hourly values over a 7-day period) = 5.11), with a peak of activity just before dawn.

4. The Fate of N. burrowsius

As pointed out by Skrzynski (1968), it is unlikely that N. burrowsius will continue to survive on the Canterbury plains with land continually being modified for agricultural purposes. He suggested that N. burrowsius was probably unable to maintain itself in these conditions and/or compete with the native and introduced fish which are abundant in artificial waterways, viz. P. breviceps, G. vulgaris, Anguilla spp. and S. trutta. However, the ability to aestivate confers an advantage on N. burrowsius, enabling it to survive in situations in which the other species could not survive, e.g. Stokell (1949) found skeletons of small eels in damp earth in which N. burrowsius was aestivating. Although there are still a number of isolated bodies of water in which N. burrowsius persists, its continued survival appears to depend on the setting up of reserves or the prevention of land modification in areas in which it is known to exist.

5. Acknowledgements

For assistance with fieldwork I am indebted to G. A. Eldon of the N.Z.M.A.F., M. Keillor of the Waitaki Valley Acclimatization Society, and T. Lake. I would also like to thank the many other people who answered circulars and provided information on possible mudfish localities. I am grateful to members of the Canterbury Exotic Fish Society for their assistance in attempts to breed the mudfish.

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Only references not included in the main reference list are listed here.

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Appendix 2

SOURCE LOCALITIES FOR THE GALAXIIDAE USED IN THE BRAIN STUDIES

(S)= South Island, (N) = North Island of New Zealand.

Species	Locality
G. vulgaris	River Glentui, Canterbury, (S).
G. maculatus	Purau Stream, Canterbury, (S). Okuru River, Westland, (S). Lake Waiparera, Northland, (N).
G. fasciatus	Wainui Stream, Canterbury, (S). Jackson Bay Creek, Westland, (S). River Kaueranga, South Auckland, (N). Rayners Bay Stream, Lake Okataine, Bay of Plenty, (N).
G. argenteus	Tributary of Hutt River, Wellington, (N).
G. brevipinnis	Lake Rotoroa, Nelson, (S). Arawata River, Westland, (S).
G. postvectis	Buller River, Westland, (S). Tributary of Waikanae River, Wellington, (N).
G. paucispondylus	Porter River, Canterbury, (S).
G. divergens	Tributary of Horomanga River, Rangitaiki System, Bay of Plenty, (N).
G. prognathus	Wilberforce River, Canterbury, (S).
G. gracilis	Upper Rototuna Lake, Northland, (N).
N. burrowsius	Localities 3, 4, 10, 11, 12, 13, 18 (see Appendix 1), Canterbury, (S).
N. apoda	Tributary (draining swamp) of Whataroa River, Westland, (S). Pirinoa River, Wairarapa, (N).
N. diversus	Swamp at Hikurangi, Northland, (N).